The effect of behaviour on evolutionary mechanisms in Gallinaceous birds

by

Alan Lill, B.Sc. (A.R.C. Poultry Research Centre, West Mains Road, Edinburgh 9 Scotland.

Thesis presented for the Degree of Doctor of Philosophy of the University of Edinburgh in the Faculty of Science, March 1966.

"This gentlecock was master in some
measure
Of seven hens, all there to do his
pleasure.

She with the loveliest dyes upon
her throat
Was known as gracious Lady Pertelote.

He feathered Pertelote in wanton
play
And trod her twenty times ere prime
of day.".

Geoffrey Chaucer, "The Canterbury Tales" (originally published c. 1487)

Contents

CHAPTER I

Introduction.

In considering the evolution of behaviour, we are concerned with discovering two things, namely the course evolution has taken and the mechanisms which have brought it about. The solution to the former problem is currently being sought through comparative behaviour studies of closely related species, based on the determination of homologies (Baerends, 1958). Such studies, notable amongst which are those of Lorenz (1941 and 1950) on ducks, Tinbergen (1959) and his co- workers on gulls and terns, and Baerends and Baerends- Van Roon (1950) on cichlid fishes, not only elucidate the evolution of the behaviour patterns themselves, but also the affinities of the species studied. The second problem is being approached in two major ways; one being through the study of the genetic regulation of species- specific behaviour, the other by examining the effects of selection on the evolution of behaviour.

The present work is allied to the last- mentioned approach, since it is concerned with the role of behaviour in effecting evolution, particularly with regard to the splitting up, divergence, and isolation of populations. In addition, the effects that behaviour may exert on the population structure and density through the breeding system structure have also been examined to some extent.

In a monumental series of papers, Sewall Wright (1921, 1932, 1935, 1938 and 1940) discussed the concept of effective

population size and the importance of the breeding structure of populations in relation to their evolution. The effective size can have considerable influences on the genetic constitution of subsequent generations. WRIGHT pointed out that it very often differs from the apparent population size, since it represents only those animals in a population that actively contribute genes to subsequent generations.

Wright (1932) claimed that the optimal population structure of a species for the most rapid rate of evolutionary change is theoretically one in which there is division into largely inbreeding sub- populations but with a limited degree of gene-flow between such sub-units. Such a population structure would be the most effective mechanism for 'trial and error' in the field of gene combinations. Evolution in a large panmictic population could only be by new mutations which are favourable immediately they appear, and such evolution is necessarily slow. On the other hand, reduction of population size below a certain relation to the mutation rate and severity of selection is likely to effect extreme inbreeding and the deterioration and homogeneity of a closely inbred population. The superiority of the sub-divided population structure lies in that there is a good chance that one local sub-population will reach a new adaptive "peak" (in the field of gene combinations) and will then "pull the rest of the species with it towards the new peak" by crossbreeding. Wright claimed that the average adaptiveness

of the species advances more effectively under inter- than under intra- group selection. Thus one of the inherent advantages of the sub-divided population is the retention of greater genetic flexibility, whereas under conditions of panmixia one genotype establishes a lead over others and becomes fixed. Wright stated that there is considerable evidence among species to support his claim. Interestingly, Popham (1947) and Blair (1953) have recently discovered what appear to be such sub-divided population structures in Corixa and Peromyscus respectively, though there is no evidence to suggest that the populations they studied were evolving at a more rapid rate than others of the same or related species.

Wright's theoretical concepts of micro-evolutionary mechanisms have found support amongst many evolutionary and genetical students (Huxley, 1945; Allee et al., 1949; Dobzhansky, 1949). The role of social behaviour in such micro-evolutionary processes has been little examined, however. Behaviour may modify the size and structure of populations through the agencies of non-random mating systems[1], inter-population aggression etc. This paper is concerned with the potential role of behaviour in population systems such as that discussed by Wright, and especially with the breeding structure of partially isolated groups and the behavioural barriers to inter-population gene-flow. It is felt that a study of the manner in which and extent to which

social behaviour affects the genetic composition of populations could elaborate and extend micro- evolutionary theory, especially the theories advanced by Wright.

Darwin first recognised and discussed the importance of reproductive isolation in evolution, and Dobzhansky (1937) coined the term "isolating mechanism" for those barriers precluding 'successful' inter- breeding between species or populations. Isolation is a conservative factor, precluding gene wastage in the production of sterile, non-viable or unadaptive hybrids, and yet also limiting the "exploration" of more and more of the possible gene combinations, and consequently decreasing the incidence of new and better adaptive genotypes. The temporal occurrence of isolation in evolution is thus critical. When it occurs at an early stage, genetic flexibility is drastically reduced, and evolution is likely to be slowed down and restricted. On the other hand, Sibley (1957 and 1961) has pointed out that hybridisation will occur if extrinsic barriers (spatial isolation) break down before intrinsic ones have evolved. Introgressive hybridisation may under such circumstances lead to 'swamping' of parental populations.

Isolating mechanisms function mainly in species maintenance, preserving the genetic discreteness of species. It is a matter of controversy as to whether assortative mating and isolation can ever effect sympatric speciation. Mayr (1963) refutes the idea, but the case is not proven either way as

yet. Recent evidence of homogamy at an intra-specific level in several avian species (Cooch and Beardmore, 1959; Goodwin, 1958; O'Donald, 1959, and 1960 a and b) necessitates some caution in the evaluation of the sympatric speciation theory. The process is probably a rare one, however, for, as Hogben (1946) has demonstrated, homogamy would need to be very intense to have much effect on evolutionary processes. Certainly positive assortative mating is potentially an important evolutionary agent, since its principle effect is to increase genetic variance (Fisher, 1930).

Of the many classifications of isolating mechanisms (Du Reitz, 1930; Dobzhansky, 1949; Schmalhausen, 1949; Allee, et al., 1949; Ripley, 1952; Mayr, 1963), that of DOBZHANSKY will be adhered to in this work. He divides them into two categories, geographical and reproductive, the former alluding to allopatric populations separated by a physical barrier, the latter to sympatric populations between which effective hybridisation is precluded by a variety of factors. The former is probably the chief factor in species initiation, though MAYR restricts his definition of isolating mechanisms so as to exclude geographical isolation altogether. MAYR does, however, draw a nice distinction between pre- and post -mating isolating mechanisms, the latter being less open to selection than the former. Rivas (1964) has introduced the term 'syntopy' to differentiate between species in contact with and having a chance to breed with other related

species, and those occupying the same area and not necessarily having the chance (sympatry). It is between syntopic species or populations that ethological isolating mechanisms act. The phenomenon is variously known as sexual isolation, psychological isolation or behavioural isolation.

Behavioural isolation, one of the most important types of isolation, occurs when there is a behavioural 'incompatability' between individuals of two separate populations, often in some aspect of courtship behaviour. Species-specific courtship patterns thus often have strong isolating value, for example, since they fail to release the appropriate response in heterospecific individual, and courtship terminates prior to coition. Isolating value may reside in one or more of many characteristics, morphological, acoustic and behavioural; a brief survey of some of the more pertinent literature is presented later (page 45).

Birds utilise mainly visual and vocal signals in courtship. Where hybrids are at a disadvantage to parental populations, isolating mechanisms are reinforced, and this results, in birds using visual signals in pairing, in the enhancement of the structures and associated behaviour patterns important in species "recognition"[2]. These are usually the dimorphic structures and behaviour patterns of the male (Sibley, 1957). Resultant upon this is increased diversity of plumage characters among syntopic species, and the extreme cases of this are seen where there is the added

effect of intra-specific sexual selection (as in many grouse, humming-birds, manakins, birds-of-paradise etc., which are polygamous, promiscuous, and display communally).

The mechanism and nature of intra-specific non-random mating has also been studied. This phenomenon is particularly marked in those gallinaceous birds exhibiting 'lek' and 'harem' breeding systems (certain grouse, pheasants and wild turkeys). Of particular interest are the evolution of such breeding systems, the selection pressures involved, and the mechanisms and functional significance of non-random mating. Data on non-random mating systems in birds are few, and a meaningful evaluation of the phenomenon and its consequences will be possible only after its thorough study in a range of species exhibiting it. The present study of non-random mating in two captive sub-species with hierarchical social organisation is an attempt to add a little to our meagre knowledge of the mechanisms involved. Some wild animals have a social hierarchy, and moreover, the resemblance of certain of the present testing conditions to 'lek' and 'harem' systems renders the present experimental material and methods a useful 'model' for detailed, laboratory studies.

Two captive sub-species of Gallus, the domestic fowl (Gallus gallus domesticus) and the Burmese Red Junglefowl (Gallus g. spadiceus) have been used in this work. Investigations of sexual isolation and non-random mating are difficult to carry out on wild species, but both the laboratory and the

field approaches are necessary in order to evaluate these phenomena fully. There are inherent dangers and limitations in carrying out evolutionary studies using domestic and captive species, but there are also advantages and useful knowledge to be gained. Due caution has been exercised in interpretation of the results and their significance. I should add that a study of non-random mating in fowls is not without relevance to poultry husbandry.

Although primarily an evolutionary study, the present work rapidly led the author into the consideration of certain fundamental aspects of animal behaviour, which are currently enjoying much attention from ethologists. In particular, it involved the investigation of species discrimination and the role of early experience in directing adult sexual behaviour to the appropriate partner. In discussing this aspect of the work, it has therefore been necessary to evaluate the present findings in the light of the theory of Sexual Imprinting, of which Lorenz and Schutz are the chief exponents. It has stimulated thoughts as to the functions of displays, the signal value of their several components and the information they convey. It has perhaps underlined how little sophisticated information we possess about the precise mode of action of visual components of display.

No student of sexual selection and non-random mating can study these phenomena at length today without forming opinions on the theory of Wynne-Edwards (1962), who ascribes to

polygamy and non-random mating in communally-displaying species the function of regulating population density. His theory of self-regulation of population density will be mentioned again at a later stage.

Like sexual behaviour, aggressive behaviour may also have isolating value. In considering the potential of aggressive behaviour as an ethological isolating mechanism in the fowl, I have assumed that aggressive behaviour can have this role in wild species. Demonstrations, however, are few, the most notable being that of Hunsaker (1962) with sympatric lizard species. Inter-specific aggression certainly occurs amongst birds (Fisher, 1964), and Lanyon (1959) argues that inter-specific aggression, manifested in inter-specific territoriality, can form a barrier to hybridisation in the early stages of speciation. Some authors disagree (see Orians and Willson, 1964) with this viewpoint, and much further work is required to settle the controversy. Within the species, populations may exist as closed social groups. It is largely unknown whether gene-flow is restricted between such groups to such a degree as to vitiate the Sewall Wrightian population model. Clearly the results of investigations of the parameters of inter-population gene-flow have an important bearing on the controversial theory of sympatric speciation mentioned earlier.

Footnotes:

1. In this study, a behaviourally-regulated non-random

mating system will be defined as one in which some individuals in breeding condition in a population do not contribute, or contribute significantly less genes than others to subsequent generation(s) due to behavioural causes. This definition thus means that most mating systems conform to this definition to some degree, but our concern here is with those species whose social organisation during the breeding phase results in elaborate and well developed non-random mating.

2. The term overt species discrimination will be substituted for species "recognition" in this paper.

General Remarks on the Literature

Certain books and papers have formed standard works of reference during this study. Hinde (1959) reviewed behaviour and speciation in birds and lower vertebrates, but perhaps the best discussion of the role of behaviour in speciation is that of Mayr (1963). The reviews of isolating mechanisms by Dobzhansky (1951) and Allee et al. (1949) are a very useful introduction to this field of study, whilst more general reviews of behaviour and evolution have been written by Tinbergen (1951 and 1963). Much useful information on communal display and non-random mating is contained in the books of Wynne-Edwards (1962) and Armstrong (1947). Cushing (1941) reviewed the role of mating preferences as a factor in evolution of birds, but an up-to-date review of this topic is now sadly needed.

This paper is largely concerned with the courtship and agonistic behaviour of the domestic fowl (Gallus g. domesticus) and Red Junglefowl (Gallus g. spadiceus). General reviews of the behaviour of the domestic fowl have been written by Guhl (1953, and 1962) and Wood-Gush (1955). For basic descriptions and analyses of courtship and agonistic patterns the reader is referred to Skard (1937), Wood-Gush (1954 and 1956) and Guhl (1962) on the Fowl, and Kruijt (1964) on the Burmese Red Junglefowl. In general I have adhered to the terminology of Wood-Gush and Kruijt, except that one additional pattern with

possible sexual significance ('head-waggling') has been identified in the domestic fowl, and I have substituted the names 'stamp-squat' and 'body-shake' for 'cornering' and 'feather-ruffling' respectively.

Material

Two true breeds, several strains of these breeds and some crossbred (Broiler) strains of domestic fowl have been used:-

Brown Leghorn material:

i) 'B' strain, a standard Brown Leghorn exhibiting the typical Brown Leghorn phenotype. Designated B strain.

ii) 'Red' strain, a highly inbred strain of smaller dimensions than the standard Brown Leghorn. The breast of the hen is redder, and the male has a chestnut coloured plumage, broken only by some minor black markings. The birds are smaller than 'B' birds, and their vocalisations are generally higher in pitch. Designated R line.

iii) 'White' strain, an inbred strain, in which the typical Brown Leghorn plumage occurs in conjunction with an all over white mottle. The birds are of comparable size to 'B' birds, their vocalisations differ in pitch, tone etc., and they have the 'flightiness' of a White Leghorn. Designated W line.

White Leghorn material:

i) Sterling White Link, a vigorous, inbred strain of commercial origin, selected for laying performance. The plumage is

white throughout, the males being larger than, and the females being smaller than the corresponding sex in the 'B' strain. Designated S line.

ii) Reaseheath C strain, a highly inbred white strain, a little smaller than the 'B' birds, with characteristic pitch and tone of vocalisation and low sexual vigour. Designated RC strain.

Crossbred (Broiler)material:

Several strains, originating from a four-way cross between White Leghorn x Cornish Game x Rhode Island x Light Sussex, and bred originally as part of a genetic study of the body weight: shank length ratio. In strains great individual differences in plumage colour, comb type and other characteristics exist, such that there are very few shared comb and colour characters. Three groups of birds were used; originally a mixed strain group was used (MCBR), and some tests were also carried out with a dwarf (CBRD) strain. Latterly, only one strain has been used, namely the Alpha (ACBR) strain.

In all, several hundred birds have been experimented upon during the study period, and these have been derived from several different hatches. The strains of fowl used are shown in figure 1.

Junglefowl studies were carried out with the material at the Zoölogisch Laboratorium of the Universiteit te Gröningen, Nederland. The birds are thought to be a good, undomesticated Gallus g. spadiceus, and have been described by Kruijt (1964).

Figure 1: Some of the breeds and strains of Domestic Fowl used in the study.

(See top copy)

Most of them were in their first or second season, and all had previous heterosexual experience at the time of study. A total of approximately sixty birds were used in this two month study. Incidental observations have been made on a few other species of gallinaceous and other birds

Methods:

Domestic fowl studies:

All observations were carried out in indoor pens and cages. Cocks were generally housed in individual cages, and hens kept in enclosed pens in small groups of 6 - 15 birds. Artificial lighting was provided for 14 hours per day. Observations were carried out in enclosed pens, which varied in size from 8' x 6' to 8' x 9' to 13' x 6', though the size was kept constant for any given experiment or set of experiments. The observer watched the subjects through a 'uni-directional', dark-glass window. Trap-nests were provided, but access to these and to roosts was often precluded during short tests. All birds were incubator-hatched, and except in experiments on early experience effects, the newly-hatched birds were then kept in heated brooders until 8 weeks of age, when transfer to larger, communal cages took place. At twelve weeks old, birds were generally transferred to pens or to individual cages.

Observational records were generally written, displays being noted by means of a shorthand code. Where timing was

necessary, it was done by stop-watch, and a hand-tally was used on occasions. One important criterion of female receptivity was taken to be the sexual or solicitation crouch, in which the female crouches on her tarsi and spreads the wings laterally and horizontally. This frequently stimulates the courting cock to mount and copulation may ensue. Crouches resulting from overt aggression by the male, from bodily contact with the male, and all non-sexual (submissive) crouches were not scored. Controls were employed where necessary. Most observations were carried out in the late afternoon from 15.00. to 18.00, hours, since it has been demonstrated that sexual activity is highest during this period (Upp, 1928; Skard, 1937; Parker, McKenzie and Kempster, 1940; Long and Godfrey, 1952).

Two main methods of testing for sexual isolation which have been used extensively during the study will be described here, further experimental details will be given under the appropriate headings. Female discrimination between males of different breeds or between males of one line was tested by the 'alternate-presentation technique', in which group-penned females were presented with single males in rotation. The courtship of the males, the crouching of the females and the incidence of coition were all recorded. Male discriminations between hens of two strains or breeds were tested in a 'simultaneous-presentation situation', in which they encountered caged, cue females of the two types in a test pen. The males

were admitted singly to the pen through an entrance tunnel or door. The cue females were in two, separate, cylindrical, wire-mesh cages, equidistantly placed from the entrance tunnel. The pen floor was free of litter etc., and marked out into three areas, A, B, and C, by white lines. Areas A and B surrounded the cages, area C was a neutral zone. A and B were of equal size and were designated cage areas. The dimensions of the original simultaneous-presentation situation are given in Fig.2, and although the absolute dimensions were subsequently altered to improve the test, their relationship remained unchanged throughout the study period.

Tests usually lasted from 9 to 15 minutes. Three measures of the cocks' display to each cue hen (i.e. the display activity taking place in the two cage areas) were taken viz., the total display score, the time spent in each cage area and the amount of "waltzing" to each cue. Of these three, the last proved to be the best measure of male "preference", since it is the only display occurring in this situation that is normally orientated to a single, specific female (Fig.3). Each male was always tested twice on each discrimination, the cues being reversed in location on the second test to rule out possible directional effects. Duplicate groups of cues were used, half the males being tested on one and the others on the other, in order to gauge more effectively whether any discrimination shown was a reflection of strain or individual discrimination. Suitable inter-test intervals were employed to avoid familiarity with

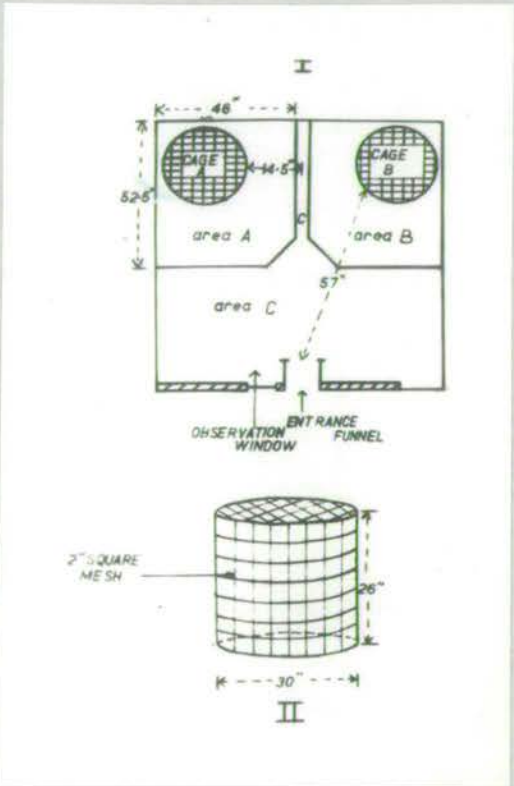

I
46"
CAGE A
14.5"
CAGE B
52.5"
area A
C
area B
57"
area C
OBSERVATION WINDOW
ENTRANCE FUNNEL
2" SQUARE MESH
26"
30"
II

Figure 2: Original simultaneous-presentation situation employed to test homogamy in males

I. Plan view of test pen

II. Cage in which cue hens were placed

All measurements in inches

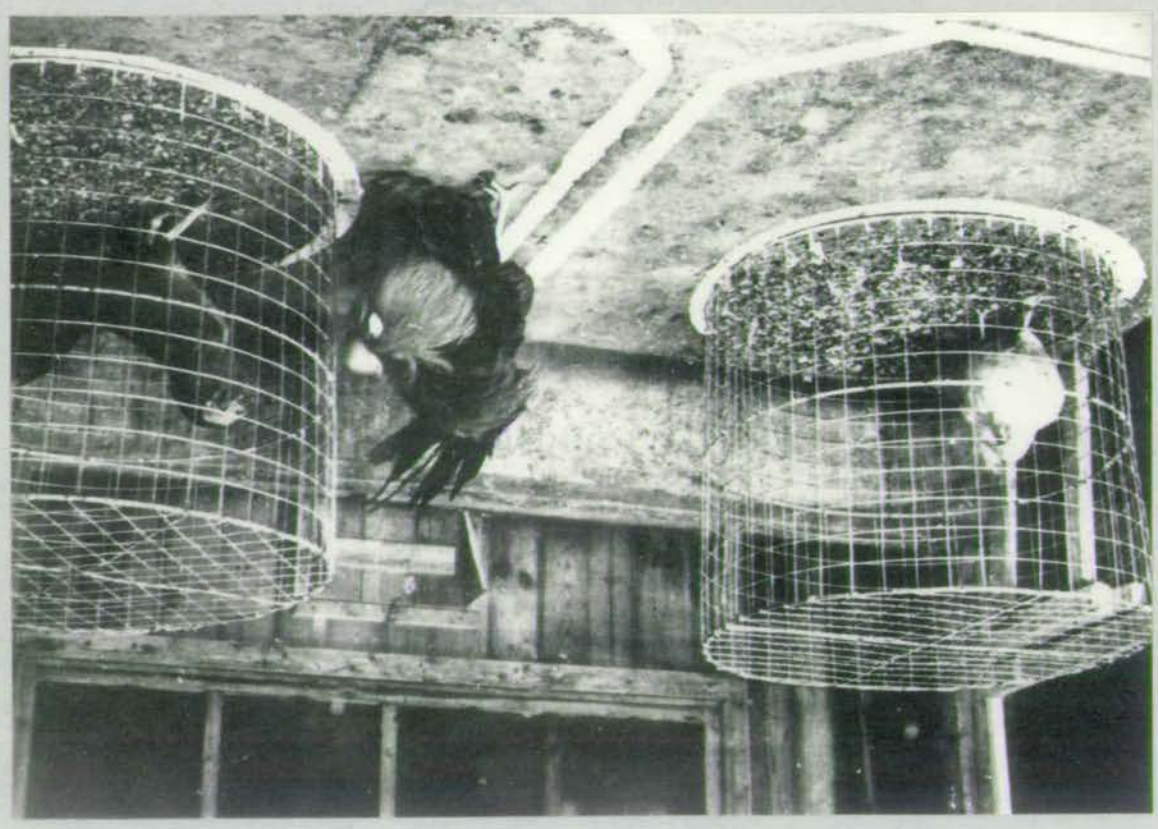


Figure 3: A Brown Leghorn male avoids the White Leghorn hen in Cage Area A and waltzes to the caged own-strain female in Area B

the test situation, and in some later tests in large pens initial orientation of courtship was also measured. The simultaneous-presentation situation was also used to test inter-strain aggressive behaviour between males.

Junglefowl studies:

Observations were carried out in large (approximately 35 metre square) outdoor cages or runs, the observer watching from an adjacent room and being concealed or visible to the birds according to the type of test in progress. Nesting took place in rooms adjacent to the runs, but during observations access to these was precluded and alternative open nests provided in the run to facilitate observation. In an attempt to standardise the experimental conditions, observations were made only on fine days. For any one experimental situation, observations were made as far as possible on consecutive days, but inclement weather sometimes interrupted the schedule. Further details of techniques are given under the relevant headings.

In both studies, birds were individually marked, either by leg rings or numbered wing-badges, in order to facilitate individual recognition by the observer. It will be seen that the main statistical tests used to evaluate the numerical data were the chi-square, correlation coefficient, analysis of variance, the t test and coefficient of variance.

Chapter II

Sexual isolation and homogamy in the Domestic Fowl

Although, as already pointed out, the number of experimental studies of sexual isolation is still comparatively small, several well documented examples exist for insects. In Drosophila, sexual isolation has been demonstrated between species, subspecies, geographical races and mutant strains; the reader is referred to excellent reviews by Patterson (1942), Spieth (1952) and Patterson and Stone (1952). Among more recent studies, that of Manning (1959) has shown that D. melanogaster and D. simulans are sexually isolated. It is evident from Drosophila studies that species discrimination, an integral process in the sexual isolation phenomenon, is generally divested in both sexes. Males may exercise discrimination by breaking off courtship with heterospecific females prior to copulation; females may preclude mounting by, or "kick off" heterospecific males. Knight, Robertson and Waddington (1956) have shown that the isolation index can be increased by direct selection, and Pearce (1960) noted that forty generations of anti-hybrid selection in melanogaster changed mating patterns and strengthened sexual isolation. As Tinbergen (1963) has pointed out, such studies may demonstrate how selection contributes to speciation.

Perdeck (1957) demonstrated the role species-specific song patterns as isolating mechanisms between two sympatric sibling species of short-horned grasshopper (Chorthippus bruneus and C.

biguttulus). Some degree of hybrid isolation was observed, since the intermediate song of F I males did not affect parental females. In the same genus, Jacobs (1953) discovered that Chorthippus montanus females respond to conspecific male calls, but not to those of related C. parallelus males. Several authors using play-back techniques with recorded calls have demonstrated the importance of such species differences in sound signals in sexual isolation in related groups (e.g. Walker, 1957; Haskell, 1957).

Hubbs (1961) has reviewed the role of isolating mechanisms in the speciation of fishes; notable studies in this field have been those of Haskins and Haskins (1949 and 1950) and Liley (1962) on poeciliid species. A wealth of information on the sexual isolation phenomenon in Anura has emanated from W.F.BLAIR and his co-workers in Texas. The Anura are typified by simple, stereotyped courtship patterns, species-specificity residing chiefly in amplexus (clasping) behaviour and courtship vocalisation. A typical example of Anuran sexual isolation studies is that of Blair and Littlejohn (1960), in which two allopatric species of Pseudacrid chorus frog were studied. Females selected the recorded calls of conspecific males rather than those of heterospecifics in a simultaneous-presentation situation. It was inferred that call divergence under allopatry would effect sexual isolation under secondary contact conditions. Bogert (1960) has reviewed the role of vocalisation as an ethological isolating mechanism in Anura, though his account is

somewhat disjointed.

Hunsaker (1962) described sexual isolation effected by social organisation in the Sceloporus torquatus lizard group. Females 'chose' the territories of conspecific males, who then drove out any intruding heterospecific male. Isolating value was divested in species-specific "head-bobbing" patterns and scents.

We know extraordinarily little about ethological isolating mechanisms in the mammals. The two outstanding experimental studies concern New World Peromyscid deermice and races of the bank vole (Clethryonomys glareolus) in the British Isles. Blair and Howard (1944) found potential sexual isolation between forms of the cenospecies Peromyscus maniculatus kept in mixed laboratory communities. Colour and scent were thought to be releasers of specific discrimination, and some degree of hybrid isolation was observed. Similarly conducted later studies failed to reveal sexual isolation between four, geographically partially-isolated sub-species of Peromyscus (Blair, 1954), but evinced potential sexual isolation between sympatric P. truei and P. nasutus (Blair, 1953). A recent study by McCarley (1964) also revealed potential ethological isolating mechanisms between sympatric but not allopatric forms of the P. leucopus cenospecies.

Godfrey (1957), using a simultaneous-presentation situation, found marked homogamy in races of the bank vole from different areas of Britain. As in Peromyscus, racial scent differences appeared to be important in discrimination. Hybrids, whilst

not discriminating significantly between the two parental forms, were discriminated against by these races. Several other factors contribute to a low adaptive value of hybrids, and GODFREY concludes that under conditions of sympatry, natural selection would probably perfect the sexual isolation existing between the races. Sexual selection studies in laboratory mice (Levine, 1958) have revealed a type of sexual isolation operating through male agonistic behaviour. It is to be expected that further studies of sexual isolation in small mammals will confirm present indications that olfactory stimuli are of paramount importance in specific discrimination.

Finally amongst avian species, it is well known that visual and vocal stimuli are the main signals operative in courtship and agonistic behaviour, and thus it is these characteristics which possess isolating value as a rule. Dilger (1956) concluded from his study of Hylochica mustelina and four species of Catharid thrush that call differences were important in isolating the species. Females of two Grackle species (Cassidix major and C. mexicanus) exhibited homogamy according to the account of a field study by Selander and Giller (1961); they discriminated between species on differences in male courtship behaviour and vocalisation. The reader is also referred to a recent account of isolating mechanisms in the Anatidae by Johnsgaard (1963). There are several recent descriptions of positive assortative mating (homogamy) at an intra-specific level in birds which

should be noted. All concern polymorphic or polyphenotypic species. Goodwin (1958) noted positive assortative mating between colour types of domestic and feral pigeon, and suggested that imprinting might be involved in its initiation. Some confirmation of his observations is furnished by the work of Warriner, Lemmon and Ray (1963), who demonstrated that parent colour influenced subsequent mate selection in male but not female pigeons. Cooch and Beardmore (1959) also found evidence of homogamy in the Blue-Snow Goose complex, whilst O'Donald (1959 and 1960) cites a similar tendency between two co-habiting colour phases of the Arctic Skua (Sterocorarius parasiticus). The importance of these findings in relation to the much-disputed sympatric speciation theory has been mentioned earlier.

Evidence of sexual isolation between breeds and strains of domestic chicken is limited. Silson (1963) has attributed some findings of Parker (1961) to assortative mating. PARKER found that low fertility resulted from Dark Cornish ♂♂ x New Hampshire ♀♀ matings in comparison with New Hampshire ♂♂ x New Hampshire ♀♀ matings, and showed that this did not result from differences in sperm quality and male interference in mating. However, the possibility that mechanical isolation (Dobzhansky, 1949) was involved was not excluded. Fisher and Hale (1956) divided a group of New Hampshire cocks into 'good' and 'poor' responders on the basis of their reactions when presented with stuffed hen models. The males had no previous experience of other breeds, but 'poor' responders subsequently exhibited

an own-breed bias in a "choice" test involving own-breed and strange-breed hens. Good responders failed to discriminate however, and the difference between the two categories of male was most marked when own-breed and white breeds were paired as cues. Subsequent tests of poor responders with mixed-breed female flocks showed that they exhibited an own-breed bias in waltzing, and similar tendencies were also observed in "no-choice" tests. Potential ethological isolating mechanisms were thus implicated, though mixed-breed flock tests are of doubtful significance due to the breed-dominance phenomenon (c.f. Crawford and Smyth, 1964).

The primary purpose of the present series of experiments was to test more fully the occurrence and potential of ethological isolating mechanisms between breeds, and strains within breeds, of Fowl. Present testing conditions bear some resemblance to natural conditions; the alternate-presentation technique used in the present work has some similarity to the condition described by Sibley (1959), in which two syntopic species, isolated throughout most of their range, hybridise in one location where the ratio of species individuals is disproportionate. Under such conditions, animals appear to mate with what would normally be biologically inappropriate partners. It is of particular interest that potentially highly effective ethological isolating mechanisms have been observed in the Fowl under such conditions, when there is considerable pressure exerted <u>against</u> sexual isolation.

As previously pointed out, the Fowl presents a useful laboratory 'model' on which to investigate intra-specific non-random mating phenomena and the problems of micro-evolution, since there are so many differing plumage types, though comparatively little breed divergence in behaviour. In the present experimental series, I have also attempted to elucidate the relative importance of male and female mate-"choice" in determining the distribution of copulation and hence the index of sexual isolation (defined later). In wild species, sexual isolation could be greatly enhanced under certain circumstances if males as well as females exhibited homogamy.

Female sexual behaviour with males of different 'breeds' in alternate-presentation situations

Material and Methods:

The sexual behaviour of a total of sixty-two B (Brown Leghorn), twenty-five RC (White Leghorn) line adult females derived from four different hatches was observed. Alternate-presentation tests of homogamy and potential sexual isolation of the type outlined on page 15 were carried out as follows:-

Test 1:

Hatch a:- Three flocks of females (one B line, one RC line and one MCBR line), each composed of ten individuals, were tested twice with each of six B, six MCBR and five RC strain males with which they were not familiar. The males were presented singly.

Hatch b:- Three female flocks, one composed of five RC hens, one of seven B hens and one of eight ACBR hens, were tested with six familiar males (i.e. the males of any one breed were the males with which the corresponding female flock of the same breed had been reared) and from two to eight 'strange' males of the same three breeds.

Test 2:

Hatch c:- A flock of fourteen B line hens was tested at twenty-three weeks post-hatching with six strange own-strain and six strange S strain males, each male being presented twice to the flock.

Hatch d:- Three flocks, each of seven B line hens, were tested once with each of four strange B and four strange S line males

in a repeat of the test alluded to in Hatch c above.

Test 3:

Two groups, each comprised of fifteen S line laying hens, were tested twice with each of six strange own-strain and six strange B strain males.

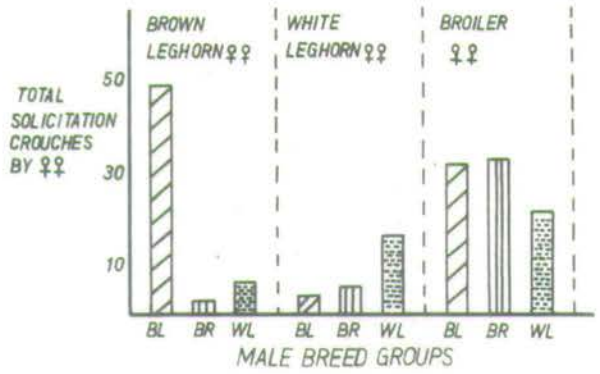
Test 4:

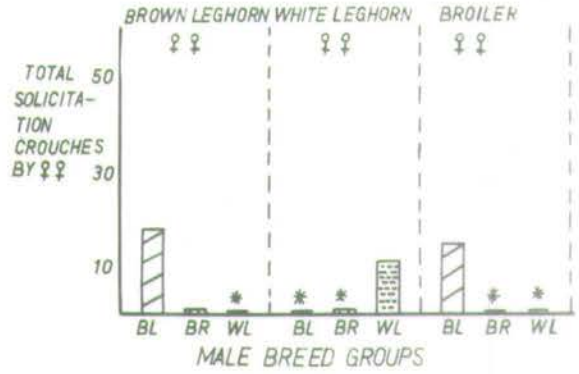
A flock of ten RC hens and one of ten B hens were presented singly, twice with each of six strange MCBR and six strange CBRD males. The RC females were those from Hatch a (Test 1), the B females were also used in another test (page 34).

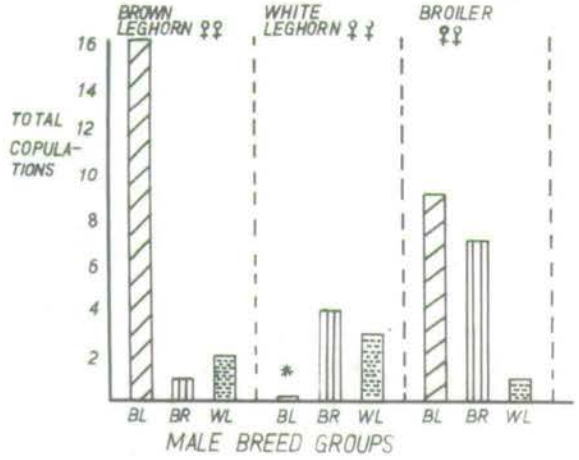
During all tests, female solicitation crouches and the incidence of copulation were recorded. (It is rarely possible to determine exactly, by direct observation only, if actual ejaculation has occurred). In certain tests, notably Test 1, complete, quantitative records of male courtship behaviour were collected. In all tests, elaborate testing schedules were chosen to avoid or minimise the effects on the results of satiation factors and differential treatment of female flocks or test males. Males were introduced into female flocks for fifteen minute periods. Apart from the MCBR and RC females of Test 1, Hatch a, whose early experience was unknown, the pre-test experience of all hens was exclusively of own-strain, heterosexual nature.

Results:

The results of all tests (1-4) are summarised in figures 4 to 7.


BROWN LEGHORN ♀♀
WHITE LEGHORN ♀♀
BROILER ♀♀
TOTAL SOLICITATION CROUCHES BY ♀♀
50
30
10
BL BR WL BL BR WL BL BR WL
MALE BREED GROUPS


BROWN LEGHORN
WHITE LEGHORN
BROILER
♀♀
TOTAL SOLICITATION CROUCHES BY ♀♀
50
30
10
BL BR WL BL BR WL BL BR WL
MALE BREED GROUPS


BROWN LEGHORN ♀♀
WHITE LEGHORN ♀♀
BROILER ♀♀
TOTAL COPULATIONS
16
14
12
10
8
6
4
2
BL BR WL BL BR WL BL BR WL
MALE BREED GROUPS

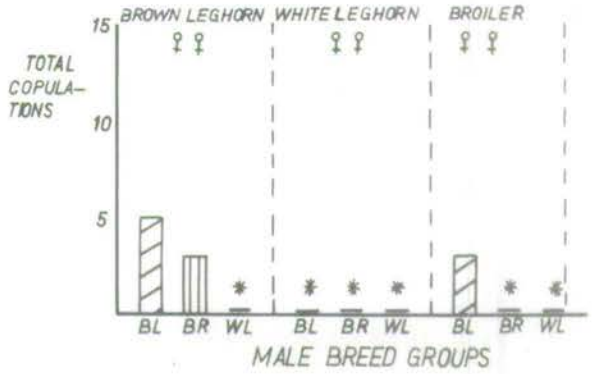

BROWN LEGHORN
WHITE LEGHORN
BROILER
♀♀
TOTAL COPULATIONS
15
10
5
BL BR WL BL BR WL BL BR WL
MALE BREED GROUPS

Figure 4: Responses of females to males of different 'breeds' in alternate-presentation situations (Test I, Hatches a and b)

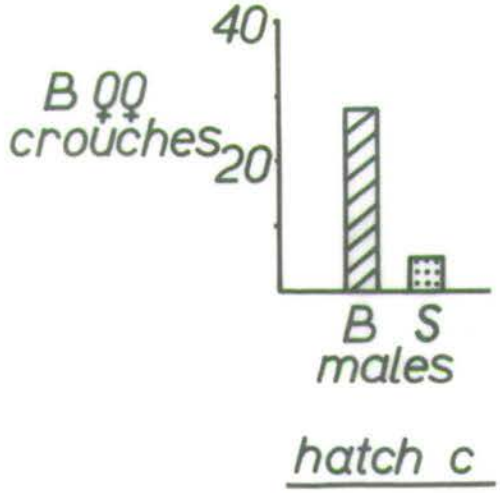
Hatch a (left), Hatch b (right)

Asterisks = zero readings

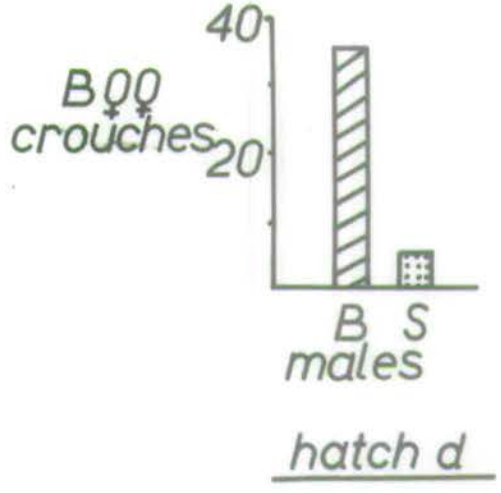
BL = Brown Leghorn (B line)

WL = White Leghorn (RC line)

BR = Crossbred birds



hatch c



hatch d

Figure 5: Solicitation of and copulation with White Leghorn (S line) and own-breed males by Brown Leghorn (B line) females (Test 2, hatches c and d)

B = B line

S = S line

Results for the three hatch d flocks pooled

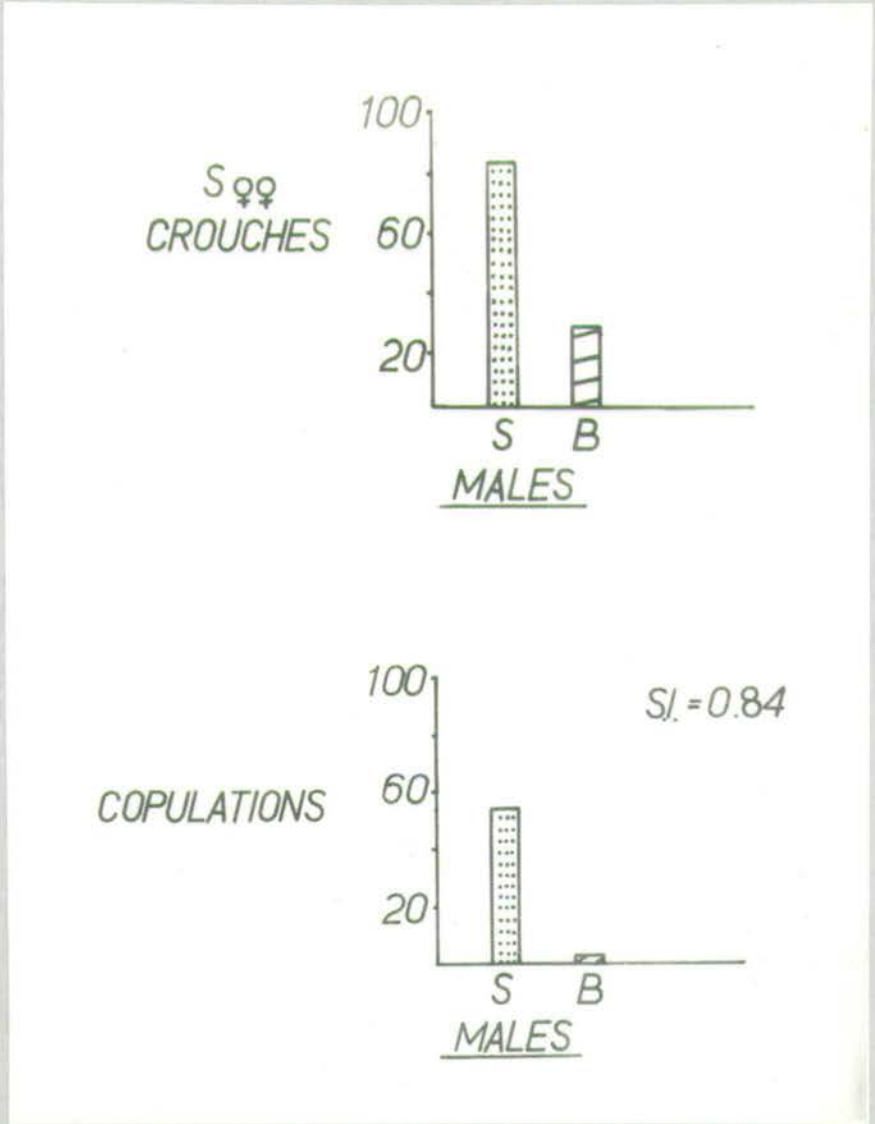

100
S ♀♀
CROUCHES
60
20
S
B
MALES
100
S.I. = 0.84
COPULATIONS
60
20
S
B
MALES

Figure 6: Solicitation of and copulation with own-breed and Brown Leghorn (B line) males by White Leghorn females (Test 3)

B = B line

S = S line

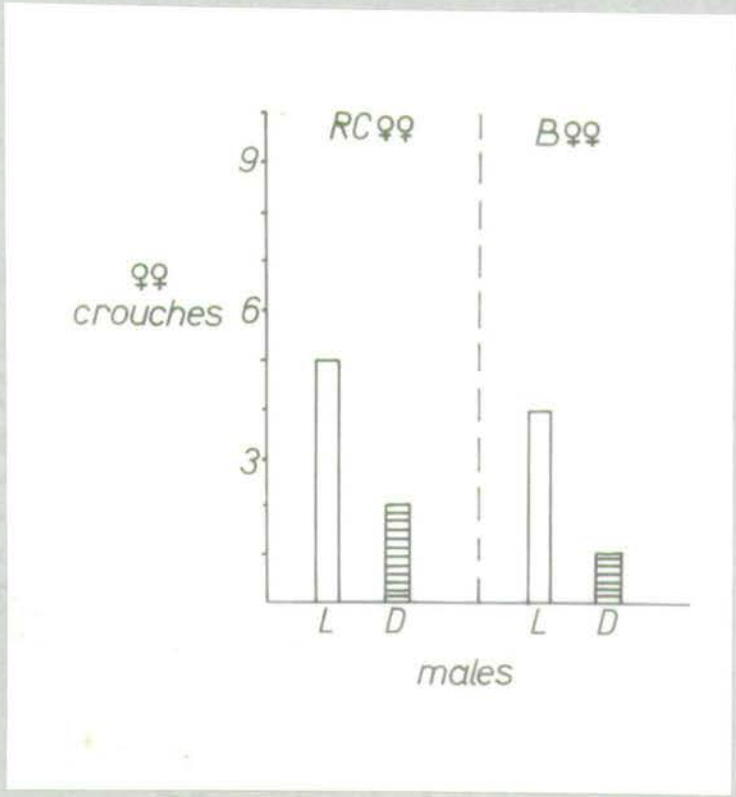

RC♀♀
B♀♀
9
♀♀
crouches
6
3
L
D
L
D
males

Figure 7: Solicitation of normal and dwarf Crossbred males by Brown and White Leghorn females (Test 4).

Test 1:

Hatches a and b:-

In both hatches, Brown Leghorn (B line) hens solicited own-breed cocks significantly more than either White Leghorn or Crossbred cocks (p in both cases $<.05$), but did not discriminate between the latter two breeds. In Hatch a, neither White Leghorn nor Crossbred hens discriminated between the three male groups significantly; however, in Hatch b, White Leghorn hens showed a significant own-breed bias ($p <.05$), whilst not discriminating between the other two breeds. Crossbred hens of Hatch b, which were of a different strain to those of Hatch a, solicited Brown Leghorn cocks significantly more than cocks of either of the other two breeds, between which they did not discriminate.

In Hatch a, copulation frequency between Brown Leghorn males and females significantly exceeded that between Brown Leghorn females and MCBR or White Leghorn males ($p <.05$). No significant differences in copulation incidence between the male groups and the different female groups was observed in Hatch b ($p >.05$); the difference between the two hatches with respect to the significance of the level of Brown Leghorn x Brown Leghorn copulation was attributable to the comparatively inefficient copulatory technique of the younger Brown Leghorn cocks of Hatch b, whose experience with receptive hens was less than that of Hatch a males. But these younger males had more incomplete matings with own-breed hens than with either of the other two breeds. In neither hatch was there an overall

correlation between the observed female solicitation distribution and the incidence of copulation.

Despite the lack of a significant own-breed bias in solicitation behaviour of Hatch a White Leghorn hens, there was a tendency in that direction. These females were substantially older than their counterparts of Hatch b and sexually unreceptive. It seems likely that more protracted tests with them may have revealed a significant own-breed bias. Thus the Brown and White Leghorn hens of both hatches discriminated in essentially the same manner. Whether the difference in the results obtained with Crossbreed females of the different hatches had a genetic or experiential basis is unknown. It should be pointed out at this juncture that the foregoing description of Hatch b female responses refers to their behaviour with males of the 'familiar' category. However, these males had been removed from their respective female flocks some weeks prior to the start of testing. Moreover, that females of this hatch were really discriminating at a breed rather an individual level was confirmed by the tests with 'strange' individuals, which yielded essentially the same results. The similarity of results in the two hatches indicates that the phenomenon of own-breed bias is relatively repeatable.

Some further observations of the behaviour of females with males of the three breeds illustrate the high level of discrimination made by the hens, and that visual cues appeared to be important in this process. Brown Leghorn

and Crossbred hens of Hatch b, responded in an extremely aggressive manner to Crossbred and White Leghorn males as soon as they entered the pen and prior to their displaying. Crossbred cocks established dominance over these female groups, but were subsequently avoided by the hens; the White Leghorn males rarely established dominance over these female groups, and exhibited fleeing responses throughout the tests. On a few occasions, these males had to be prematurely removed from the Crossbred female flock to avoid their being seriously wounded. Similarly, White Leghorn females discriminated between males immediately upon their entry into the test pen, fleeing from all except own-breed males, which they immediately approached. Avoidance of other males continued throughout tests. White Leghorn males exhibited a high latency to approach and court own-breed females, but generally did so after a lapse of a few minutes. One interesting pattern of aggressive behaviour was seen especially, though not exclusively, in RC females when presented with males of Crossbred stock in Test 1; they pecked aggressively at the feet of the males after their initial fleeing tendency had waned. The causation of this pattern is to some extent obscure, but it was noticed that although it was occasionally directed towards homogamic males, it was always more vigorous and prolonged when heterogamic males were presented. Several of the above observations would suggest a female discrimination based, at least partially upon visually perceived, physical characteristics of males

rather than upon behavioural ones.

Test 2:

Hatches c and d:-

The results for the three Brown Leghorn flocks of Hatch d were pooled, since all the groups exhibited similar solicitation distributions. Brown Leghorn females of both hatches solicited own-breed males significantly more than S line White Leghorn males (p in both cases $< .01$). The general level of copulatory behaviour in both hatches was too low to permit statistical analysis, but the tendency paralled that described for solicitation distribution above. The initial reaction of Brown Leghorn females to S line males also matched that shown by females of the same breed to RC males in Test 1, in that a strong tendency to flee from and subsequently avoid the males was observed.

Potential unilateral sexual isolation[2] existed between the B and S lines, precluding a significant level of gene-flow from the latter to the former.

Test 3:

The results for the two flocks of yearling S line females were extremely similar, and were pooled for analytical purposes. S line females discriminated between own-breed (own-strain) and Brown Leghorn males, soliciting the former significantly more than the latter ($p < .01$). Some tendency to flee from Brown Leghorn males was observed. The copulation incidence between

White Leghorn males and females was also significantly higher than that between the White Leghorn females and Brown Leghorn males ($p < .01$). The overall index of sexual isolation[3] (based on Stalker, 1942), which is derived from the formula:- $\frac{\text{Homogamic-Heterogamic matings}}{\text{Total matings}}$, was 0.84. The potential unilateral sexual isolation observed in this test was significantly stronger than that found between any other breeds used in this series of tests. The present finding, taken in conjunction with that of Test 2, is indicative of a strong, potential, bilateral sexual isolation between the two strains involved.

Test 4:

Neither White Leghorn (RC) nor Brown Leghorn (B) females solicited the normal or dwarf Crossbred males differentially. The level of solicitation of both groups was very low, and copulation did not occur. Both female groups fled from and avoided the males. This experiment was carried out in another connection, and for present purposes lacked an adequate control. Nevertheless, since I already knew that these hens were receptive to own-breed males at the time the experiment was in progress, the result perhaps serves as a further indication of the potential ethological isolating mechanisms existing between Leghorn females and Crossbred males. It is for this reason that the results reported here are presented.

In summary, it was apparent that potential sexual isolation existed between most of the breeds studied in this series of

experiments. The results, where tested, appeared to be essentially the same in similar birds derived from separate hatches but subjected to the same sort of juvenile social environment.

The one real exception to the general tendency towards homogamy in females reared under conditions of own-strain, heterosexual experience as juveniles, is that of the ACBR females of Hatch b, Test 1. That they solicited Brown Leghorn males significantly more than others was not attributable to a greater releasing valency (of female sexual solicitation behaviour) of "brown-ness" *per se*, since these females did not solicit the brown individuals amongst the own-breed males significantly more than others. In a previous paper, (Lill and Wood-Gush, 1965), it was suggested that this "preference" for Brown Leghorn males which ACBR hens exhibited might represent an innate preference for 'wild type' (with all the attendant evolutionary significance), because Brown Leghorns closely resemble Red Junglefowl (*Gallus bankiva*), one of the supposed ancestral fowls. At the time of writing, I have not been able to test rigorously whether this "preference" is truly innate, but results obtained more recently (and presented later) suggest that this is unlikely.

Footnotes:

1. For the purposes of presentation of this set of experiments, the Crossbred material has been referred to as a *breed*. This designation has been assigned to this material simply to

signify that the differences between Crossbreds and pure breeds are as great as those between pure breeds, and greater than those between strains of one breed.

2. Potential unilateral sexual isolation is used to describe the situation in which copulation between two breeds or strains is restricted by the behaviour (homogamy) of individuals of one of the two breeds only. Where the behaviour of both breeds restricts or precludes inter-breed copulation, the situation will be designated potential bilateral sexual isolation.

3. The sexual isolation index can range from +1.0 (complete isolation) to zero (no selection expressed) to -1.0 (absolute heterogamy). It is, in effect, a mathematical assessment of the efficacy of behavioural factors which restrict or prevent inter-specific (in the present case, inter-breed) gene exchange. Smith (1954) extends the concept to reproductive isolation index, to cover non-behavioural factors having similar affects on gene-exchange.

Female sexual behaviour with males of different strains of one breed in alternate-presentation situations

The main purpose of this set of experiments was to determine whether the type of discrimination observed in female solicitation of males of different breeds was also apparent at an inter-strain level, where differences in behaviour and morphology, though evident, are less pronounced.

Material and Methods:

The solicitation behaviour of a total of eighteen B (Brown Leghorn) strain and fifteen S (White Leghorn) strain females was observed during two alternate-presentation tests of homogamy and sexual isolation, as follows:-

Test A:

Two flocks, each comprised of nine, laying B strain females, were tested twice each with each of four males of three Brown Leghorn lines, B, Red and White. Tests lasted fifteen minutes each, but since one Red line and one White line male had to be excluded for two and one tests respectively due to illness, statistical tests of the significance of assortative crouching and copulation were based on mean figures. The females lacked experience of Red and White line birds, but had juvenile, own-strain, heterosexual experience. The same measures were taken as in the previously described experiments.

Test B:

A flock of fifteen S (White Leghorn) females were tested

similarly twice with each of five own-strain cocks and five RC strain cocks. In plumage colour and morphological characteristics, these two strains are more similar than the three inbred Brown Leghorn lines alluded to above.

Results:

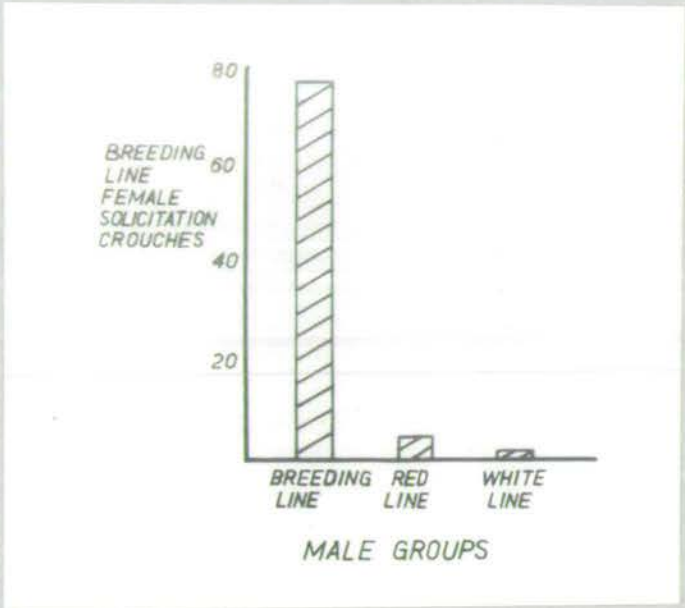
Test A:

The results for the two flocks were pooled since they were considered to be very similar. An overall significant variance in female solicitation of the three male groups was observed ($p < .05$ in an analysis of variance). B strain hens solicited own-strain males significantly more than either Red or White strain cocks ($p < .05$), but did not distinguish between the latter two strains (figure 8). A similar distribution of copulation was observed, which was significantly non-random at the five per cent level. The distribution of female solicitation behaviour and of copulation were significantly correlated ($p < .05$). Significant, potential, unilateral sexual isolation was thus observed between B and R and W lines.

Test B:

The results are given diagrammatically in figure 9. Solicitation of, mounting by, and copulation with S line males were all significantly greater than the corresponding interactions between S females and RC males. The sexual isolation index was 1.0 (i.e. absolute homogamy occurred).

Since many S line cocks displayed actively and several RC


80
60
40
20
BREEDING LINE FEMALE SOLICITATION CROUCHES
BREEDING LINE
RED LINE
WHITE LINE
MALE GROUPS

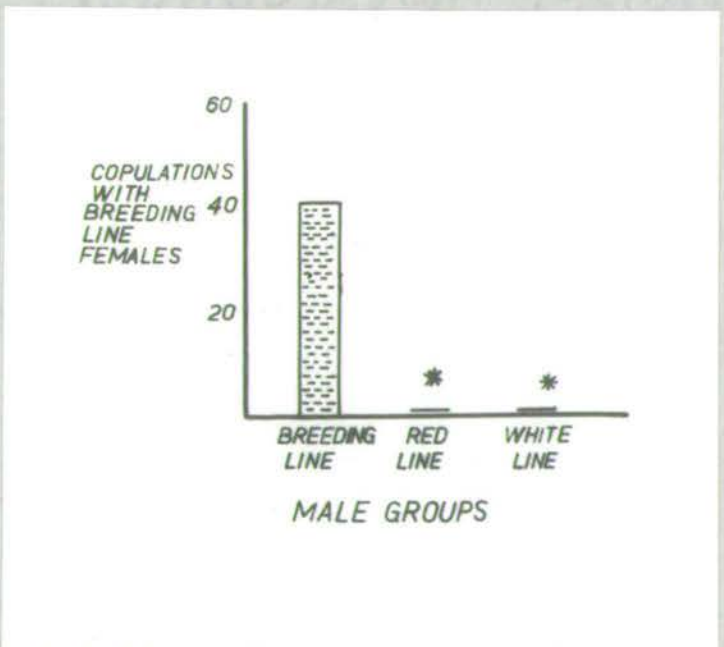

60
40
20
COPULATIONS WITH BREEDING LINE FEMALES
BREEDING LINE
RED LINE
WHITE LINE
MALE GROUPS

Figure 8: Solicitation of and copulation with males of three Brown Leghorn lines by females of the B line of Brown Leghorns

Asterisks - zero readings

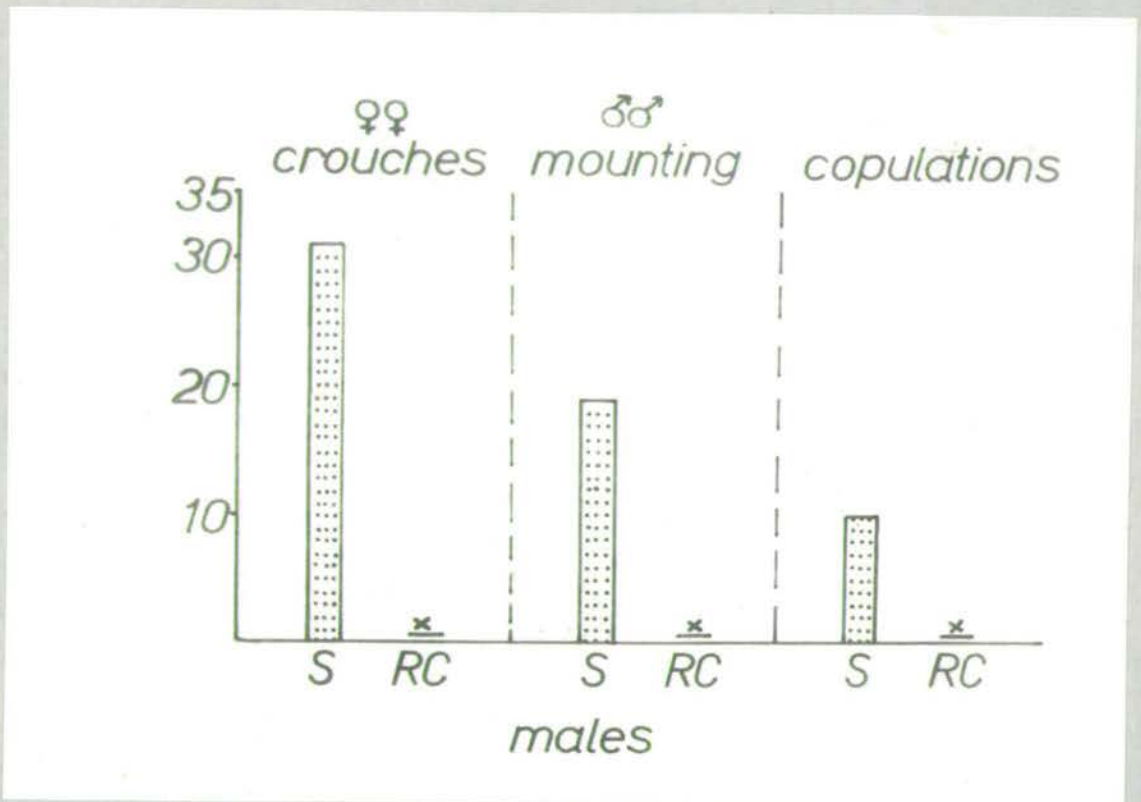

♀♀
crouches
♂♂
mounting
copulations
35
30
20
10
S
RC
S
RC
S
RC
males

Figure 9: Interactions between S strain females and S and RC strain males presented alternately

Crosses indicate zero readings

line males failed to do so, the importance of quantitative strain differences in male courtship display as a cue in female discrimination could not be ruled out. However, such differences were not the only factors upon which discriminations were based. S line females responded aggressively to most RC males, often immediately upon their entry into the test-situation; this type of behaviour was never orientated towards own-strain males. Most RC cocks elicited "fearssquawks" in one or more S females, and occasionally elicited fleeing also; S males never evoked such behaviour. Finally, those RC males which did display and court vigorously did not elicit solicitation.

The present results indicate that discrimination was based at least to some extent upon strain-specific characters other than quantitative courtship and plumage colour differences. Similarly, in Test A, the observation that B females often crouched to own-strain cocks immediately they entered the test-situation and prior to display onset, but never responded to heterogamic males in like manner, is indicative of a discrimination by females based to some degree on strain characters other than courtship behaviour.

It is clear that the homogamic tendency of females is as significant at inter-strain levels as at inter-breed levels, and that at both levels it could cause a considerable degree of sexual isolation.

Finally, it should be noted that in Test 3 (page 30), there was evidence that another type of ethological isolating

mechanism might occasionally be in operation in the domestic fowl. In this test, (see figure 6), only four S♀♀ x B♂♂ copulations occurred. This was sometimes due to interruption of copulatory behaviour after treading by the male concerned; on several occasions, however, I witnessed B line males complete the mating pattern without intromission. The cause did not appear to male inefficiency, but a failure on the part of S females to deflect the tail laterally, presumably a necessary prerequisite if cloacal contact is to take place between the sexes. On one occasion a male ejaculated on the female's back. Tail deflection failure was never observed in S♀♀ x S♂♂ matings; mechanical incompatability of genitalia was not involved, since some normal copulations between the strains were seen on that and other occasions. Tail deflection failure thus appeared to be attributable either to active discrimination by the female or to strain differences in male trampling behaviour. Whatever the causation of this behaviour, it is tentatively suggested that this behaviour constitutes a secondary type of ethological isolating mechanism, enhancing the effects of homogamic solicitation behaviour in precluding cross-mating between breeds.

Male sexual behaviour with females of different breeds and strains in alternate-presentation situations

During the course of many alternate-presentation tests designed to determine whether groups of females exhibited homogamy under such conditions, records of the courtship of many males with females of differing breeds and strains were obtained. Although certain quantitative breed and strain differences were observed between males, they did not appear to court females of different breeds or strains differentially under "no-choice" conditions as a rule (evidence of this will be presented in Chapter III). These remarks pertain to cocks of own-strain, heterosexual juvenile experience (hereinafter abbreviated to normal experience).

Only two exceptions have been observed. It will be remembered that some such apparent discrimination was recorded for RC males in Test 1 (page 29). However, it was not clear whether such discrimination was exhibited by these males in their initial tests or only in their later tests as a result of experience in initial tests. Casual A-P tests of a few, young (8 month) S line cocks did reveal that on occasions some discrimination can occur. These males had been reared exclusively with own-strain siblings, and in their initial A-P tests with S and B females at 8 months post-hatch, they courted own-strain hens, but reacted aggressively to heterogamic females. This discrimination rapidly reached extinction with increasing sexual experience, and has never been seen so clearly in other, later material.

Under A-P conditions, in which females exhibit homogamy, males generally court females of different strains and breeds in a random manner.

Male sexual behaviour with females of different strains and breeds in simultaneous-presentation conditions

In order to test whether sexual isolation in chickens could also be strengthened by a homogamic tendency on the part of males, cocks were tested under true "choice" as apposed to "no-choice" conditions. Under conditions of true syntopy there is also, in effect, often a choice between conspecific and heterospecific individuals. It is impracticable to test cocks for homogamy merely by releasing them into mixed-strain or mixed-breed flocks of females, since in the Fowl, male homogamy would be obscured under such conditions by female homogamy and the breed-dominance phenomenon (c.f. Crawford and Smyth, 1964). Accordingly the technique referred to earlier (page 15) was adopted, since it precluded these latter effects and facilitated the analysis of non-random courtship tendencies of males. This involved measuring the male courtship of each of two, live, caged hens with which males were confronted simultaneously in a test-pen.

Material and Methods:

During this study, a total of forty-two B (Brown Leghorn), nineteen S (White Leghorn) and six ACBR (Crossbred) males were tested under simultaneous-presentation conditions on one

or more of six discriminations. All males had exclusively own-strain, heterosexual experience prior to testing. Some findings referred to later indicate that differential activity levels of cue females probably exert little effect on the orientation of male courtship in this situation. Cue females were never observed to respond sexually to courting cocks under these conditions, and very rarely in an aggressive manner. Cue female vocalisation was minimal, and males were thus presented, in effect, with physical (morphological) stimuli only. The males tested were derived from six, separate hatches. It was pointed out earlier that no two Crossbred birds were alike in plumage colour. In discriminations involving ACBR cue females, therefore, tests were duplicated or triplicated using cue female Crossbreds of different plumage colour to further ensure that observed discriminations were of breed rather than individual characteristics. In tests of hatch a, e and f males and in one test with hatch b males, grey and brown Crossbred cues were used. In one test of hatch b males, a white cue ACBR female was used in addition. The test involving the white cue is indicated in figure 10.

Results:

The findings of this series of tests are illustrated in table 1 and figure 10.

Certain general features of the results should be mentioned

Courtship behaviour of cocks with females of different breeds and strains under simultaneous-presentation conditions

DISCRIMINATIONS

Strain/ Males	Hatch	No. of Males		ACBR: B		ACBR: RC		ACBR: S		B: RC		B: S		RC: S	
			IO:												
B	a	6	W :	63	100	165	1			132	1				
			TD:	214	380	450	37			454	73				
			T :	1575	3447	4536	571			4571	922				
B	b	11	IO:												
			W :	470	540†			581	73			434	43		
			TD:	979	1494			1129	289			1086	202		
B	c	9	IO:												
			W :							183	6				
			TD:							629	83				
			T :							6249	940				
B	d	16	IO:									27	5		
			W :									276	30		
			TD:									592	148		
			T :												
TC	e	6	IO:												
			W :	11	1	22	20			2	30			31	15
			TD:	104	85	147	261			36	325			273	198
			T :	1317	1581	1247	3526			376	4297			4658	3217
ACBR	f	6	IO:												
			W :	63	43	101	26			65	20				
			TD:	284	184	450	127			323	98				
			T :	3131	1895	4792	1162			3830	1195				
S	g	15	IO:												
			W :									29	484		
			TD:									111	1052		
			T :									23.5	186.2		

			IO:					
S	g	4	W :				2	6
			TD:				2	106
			T :				16	174

Legend: IO = initial orientation of courtship
W = waltzes to cues
TD = total displays to cues
T = time spent in cage areas (in minutes or seconds)

+ indicates use of white (as well as grey and brown) ACBR $\underset{++}{oo}$ cue.

STRAIN	HATCH	NO. OF MALES	DISCRIMINATIONS					
			ACBR : B	ACBR : RC	ACBR : S	B : RC	B : S	RC : S
B	a	6	B	ACBR		B		
B	b	11	B		ACBR		B	
B	c	9				B		
B	d	16					B	
RC	e	6	NOT SIGNIFICANT	RC		RC		NOT SIGNIFICANT
ACBR	f	6	NOT SIGNIFICANT	ACBR		B		
S	g	15					S	
S	g	4					S	

Figure 10: Summary of data in Table 1

Triangles indicate a significant bias in courtship, and direction of bias indicated within triangles. Triangle size proportional to level of significance of bias beyond 5% level, which was taken as criterion of significant bias.

first. Firstly, in no case did significantly different orientations of the various measures of courtship taken occur within a single test. Secondly, where ever a test was repeated with males of a different group or hatch, the results were significantly similar, indicating a repeatability of discrimination when all birds were subjected to a similar juvenile social environment. No directional tendencies were observed on the part of males, and since male groups tested with the different cue female groups responded in highly similar ways, it was concluded that discriminations were based on breed or strain rather than individual characteristics. Accordingly, data for all males of a strain performing any one specific discrimination were pooled with some confidence. Data were analysed by the t test of significance, the 5% level being taken as the criterion of significance. Many significant discriminations were apparent at the 0.01 and 0.001 levels however. The main conclusions can be summarised as follows:-

1) Generally speaking, males discriminated between breeds in simultaneous-presentation conditions. In the only test involving a discrimination between rather similar strains of one breed, RC males failed to distinguish overtly between the cue strains (c.f. results for a similar test on S line females, page 35.)

2) In all tests except two, males exhibited significantly homogamic courtship tendencies in discriminations involving own-strain cue females.

In the two exceptional cases, no significant discrimination occurred.

3) In all tests except one, males also discriminated between two heterogamic breeds to a significant degree.

4) Taking into account the differences in male group size, there was an overall general tendency for discrimination to be strongest when plumage colour disparity between cue breeds was greatest. Thus, with one exception, discrimination was less significant or not significant on the ACBR:B and RC:S tests than on others.

5) In tests not involving homogamic cues, both Crossbred and Brown Leghorn males courted the breed closely resembling their own in plumage colour significantly more than the other (i.e. than White Leghorn). White Leghorn cocks did not exhibit non-random courtship in such tests. The results substantiate the finding of Fisher and Hale (1956), who noted that White Leghorn females elicited least sexual behaviour in all but own-breed males. It was not entirely clear whether the observed 'preference' of Brown Leghorn and Crossbred males in such tests were due to the stronger releasing valency of Crossbred and Brown Leghorn females respectively, or to fleeing tendencies elicited by White cues. The difference is a subtle one, and there is some evidence in my material that white does elicit "fear" in non-white birds to a greater extent than other heterogamic colours. The problem will be referred to again in a later section.

6) The results indicated that males, like females, can distinguish between breeds in the absence of behavioural cues;

like females, they appeared to respond to breed differences in plumage colour.

Conclusions

Potential ethological isolating mechanisms were observed between 'breeds' and strains of domestic fowl, based on strong tendencies of individuals of both sexes (of normal experience) to exhibit positive assortative mating behaviour. Non-random solicitation of males by females exerted a strong, but not absolute, control on the incidence of copulation in alternate-presentation conditions. Females of one 'breed' (ACBR) solicited heterogamic males significantly more than others. Whereas females discriminated between strains of one breed, males failed to do so in the one test in which this was investigated. Males generally did not exhibit overt breed discrimination in alternate-presentation conditions, but did so markedly under simultaneous-presentation conditions. Results suggested that both sexes discriminated to some extent upon specific morphological and colour characteristics of breeds. Results obtained for males were reminiscent of those reported by Fisher and Hale (loc. cit.). Where experiments were carried out with similar birds derived from different hatches, the results were essentially similar.

CHAPTER III

An analysis of the isolating value of strain and breed specificity in the Fowl

Before discussing current knowledge of species discrimination (or "recognition"), a brief terminological clarification is necessary. The term 'releaser' was applied by Lorenz (1935) to stimuli from individuals which release innate responses in other individuals. Tinbergen (1951) elaborated this term to 'social releaser', since it generally applies to characteristics of conspecifics which release innate responses in individuals. At the time of writing, I am not entirely sure whether breed and strain discrimination in chickens is innately or experientially determined (particularly in females), and so use of the term 'releaser' will be avoided. The difficulty lies in finding a suitable substitute. It is proposed to adopt the general term 'stimulus', used rather in the manner adopted by many modern American psychologists (Hilgard, 1957) who adhere to the 'Stimulus-Response' theory, in order to avoid confusion. Similarly, the term 'stimulus valency' will be used rather in the sense that Tinbergen (1951) uses 'releasing value' in connection with efficacy of releasers of innate responses. HILGARD defines 'stimulus' thus:-

"Any objectively describable situation or event (whether outside or inside the organism) that is the occasion for the organism's response".

Whilst 'stimulus' is not entirely satisfactorily for present

purposes, it has the advantage of non-specificity which the current state of this study demands.

The level of motivation often determines the degree of sensory stimulation required to evoke a given response (i.e. motivational level may affect stimulus valency). Implicit in overt breed discrimination is evocation and orientation of responses by stimuli.

Characteristics possessing isolating value are species-specific and highly specialised as a rule. Specific discrimination, even if innate, is unlikely to be a simple process dependent on relatively few stimuli, though this may be the case in some insect species where scent differences are all-important. Innate responses are generally released by comparatively simple (sign) stimuli; but, as Tinbergen (1951) points out, innate species discrimination generally depends upon the whole range of individually unselective I.R.M.'s which in toto give to species discrimination its complexity and efficacy as an isolating mechanism. The releasers themselves may be configurational rather than unitary sign stimuli. Enhancement of signal value of courtship patterns can occur through ritualisation, the main consequences of which have been summarised by Blest (1961). Ritualisation produces stereotypy and simplification, but it increases specificity of signals and hence may enhance their isolating value. The morphological structures displayed in ritualised postures often undergo specialisation also, and similarly acquire

greater isolating value.

What will be referred to as overt species discrimination is an integral process in the sexual isolation phenomenon. In different animal groups, stimuli evoking species discrimination are diverse, varied, and correlated with the predominant sensory modality of the group concerned. Isolating value is usually divested in courtship and agonistic signals; such signal patterns are purely behavioural, or morphological, or more commonly combinations of the two. In birds, visual and auditory sensory modalities are of paramount importance in species discrimination.

Acoustic signals are important in many insect, amphibian and bird courtship patterns, and can be demonstrated to have isolating value. Walker (1957), for example, observed that female tree-crickets of species in which male courtship stridulations are continuous trills (Oecanthinae) responded to the species-specific pulse rate, which varied according to ambient temperature. By recording male calls from several species at different temperatures, he was able to obtain a uniformity of pulse rate, and observed subsequent abolition of female discrimination. Vocal signals effect sexual isolation in both Anura (Bogert, 1960) and many birds (e.g. Selander and Giller, 1961) as previously mentioned. Mechanical sounds produced by wing movements possess isolating value in tsetse flies (Vanderplank, 1948), frequency being species-specific.

Chemo-sensory discrimination is important in many insects,

mammals and reptiles. Hunsaker (1962) shows that in the absence of visual cues, species discrimination was effected through the licking of femoral pore secretions in sceloporine lizards. In Drosophila, discrimination is frequently through chemical stimuli perceived during the courtship "tapping" display, though visual and auditory discrimination is involved in some species also (Spieth, 1952). Mayr (1950) and Manning (1959) demonstrated by amputating antennae and tarsi that receptors on these regions are involved in filtering chemical stimuli.

Morphological and colour characteristics are important in the sexual isolation between many bird species. A few examples include the beak hue of Taeniopygia castonotis Gould, the Australian Zebra Finch (Immelman, 1959), eye colour in arctic gulls of the Larus argentatus complex (Smith, 1962), and eye-stripe in several duck species (Collias and Collias, 1956). The literature contains many other examples, but very few of them are the result of experimental investigations.

The isolating value of species-specific behaviour patterns, whilst "obvious" in many cases, is very difficult to verify experimentally. HUNSAKER furnishes one rather beautiful example of such verification however. To test the isolating value of species-specificity in the "head-bobbing" display of related, sympatric lizard species, he built a "head-bobbing" machine with which he could simulate the form and amplitude of the display in the several species. He

found that females tended to 'select' a model with the same 'head-bob' pattern as themselves, rather than a randomly 'bobbing' model. When presented simultaneously with models bobbing like conspecifics and heterospecifics, both S. micronatus and S. torquatus females selected the model bobbing like a conspecific. In both cases, when models were inactive, selection was at random. When more complex motor patterns are involved, determination of isolating value becomes less feasible. The importance of quantitative differences in behaviour can sometimes be examined by statistical methods, as in the present work, but such differences are probably unimportant as far as wild species are concerned.

For the sake of brevity and because many pertinent observations are anecdotal in nature, a comprehensive review of the stimuli involved in species discrimination has not been presented here.

Homogamy in chickens involves overt breed and strain discrimination, phenomema which have received some attention (though not from the sexual isolation standpoint) from Douglis (1948), Potter (1949), Potter and Allee (1953), Hale (1957) Tindell and Craig (1959) and McBride (1964). These studies, which largely pertain to conditions in mixed-breed flocks or initial pair encounters, have revealed the existence of breed discrimination in the Fowl. Flock size may be a critical factor determining whether breed or individual discrimination pertains in mixed-breed flocks (Guhl, 1962). Apparently,

previous experience with another breed affects subsequent reactions to strange individuals of that breed (POTTER) in encounters occurring within the memory span of 2-3 weeks (HALE). No detailed study of the mode of discrimination has been forthcoming, though Guhl and Ortman (1953) have investigated "individual recognition" in female flocks. HALE found that colour and comb modifications to birds in mixed-breed flocks did not affect subsequent discrimination in such flocks, but had some slight affect on paired encounters on neutral territory. McBRIDE describes his two "synthetic" strains which humans are unable to tell apart but which clearly distinguish between each other.

Currently four main ethological techniques are being employed to evaluate stimulus characteristics (Denenberg and Banks, 1962). In this study, two have been used, namely modification of stimulus animals and elimination of or interference with the supposedly important sensory modalities. Extensive use of models was not practicable, though statistical techniques of analysis have been employed. Studies of the stimuli involved in species discrimination are necessarily of an eliminative nature. The techniques outlined above, though standard, are regretably if unavoidably crude in some respects.

This chapter describes an attempt to elucidate experimentally the main cues and modalities involved in breed and strain discrimination in the present material, to determine which characteristics possessing breed or strain distinctness have

isolating value. It is not intended to be comprehensive, merely to serve as an indication of the mechanisms involved or likely to be involved in this process in avian species. In particular, it is of interest to examine the basis of discrimination in a domesticated species in which many generations of artificial selection has, in so many cases, greatly reduced precisely those characters thought to be important in discrimination in wild birds. These are the dimorphic plumage characteristics of the male (Sibley, 1957). Accordingly, I have investigated the discrimination process to some extent in two breeds; in Brown Leghorns, which phenotypically resemble the supposedly ancestral Red Junglefowls, and in White Leghorns, in which the dimorphic male plumage colour patterning has been eliminated.

Some little information has been gathered on the basis of discrimination in crossbred chickens which are segregating for many characters, including plumage colour and comb-type.

The basis of overt breed and strain discrimination in the Fowl

Factors affecting discrimination by females:

In Chapter II, it was shown that discrimination between males of different breeds and strains by females was apparently based upon both behavioural and morphological stimuli. The aim of the experiments and observations described below was to indicate in further detail the stimuli important in such discriminations by females.

Material and Methods:

Most of the experiments described below were conducted on the B (Brown Leghorn), RC (White Leghorn) and S (White Leghorn) strains. Three main techniques were adopted (see page 49). Breed and strain specificity resides in numerous characters, including plumage colour, bodily dimensions and conformation, vocalisation and non-vocal behaviour, all of which have been examined to some extent. Details of birds used, numbers, and exact experimental procedures are given under appropriate headings.

i) The importance of male plumage colour and body conformation:-

The stimulus valency of these characters was necessarily examined at the intra-strain level, by determining the effects of colour and/or contour modifications of B line males on the sexual responses of B line females. This approach was used since it was not thought possible to modify strains so as to resemble other strains with any degree of precision. Approximately eight males were used per test, each being presented twice, singly to each of two or three small flocks of females (nine to twelve individuals). Test duration was fifteen minutes. Female solicitation behaviour was recorded, and the males were subsequently assigned to one of two groups of equal size. One male group was modified, the other remained as an unaltered control. On retesting, which recapitulated pre-testing, it was thus possible to assess the effect of the alteration on female solicitation behaviour.

Colour alterations involved the attachment of 'strange breed' or dyed feathers in such a way as to lie 'naturally' amongst host feathers, or dyeing of the feather zone being investigated. Previous workers have also utilised this technique (Guhl and Ortman, 1953; Hale, 1957). Dye agents used were fishermans' fly dyes, alcohol solutions of laboratory stains and stove polish. Contour alterations involved the glueing of feathers rachis outwards to the appropriate region of the host bird (an example is given in figure 11). Feathers were attached shortly before testing, remained in position throughout tests, and did not appear to affect hosts' behaviour. One colour alteration was also carried out in the RC strain, five males and ten females being used in this pilot test.

Table 2 summarises the results of B line tests. Addition of white feathers to regions other than the head and crest significantly reduced female solicitation. Results indicated that discrimination was based on the complete breed-specific colour pattern of the Brown Leghorn male, since modifications of both dorsal and ventral regions significantly reduced female solicitation in comparison with controls. The results of tests d and e are to some extent anomalous; it is dubious whether difference in dye colour was important in this respect, but it should be noted that e involved a more complete abolition of the dorsal colour pattern. The two results, moreover, tend in the same direction. The efficacy of white

Figure 11: Brown Leghorn male with white feathers attached rachis outward to hackles (photographed some time after termination of test)

TABLE 2

Affects of colour and contour modifications of B males on overt strain discrimination by B line hens

Test No	Modification	Area Modified	%age fluctuation in ♀♀ crouching pre- and post modification. To control ♂♂	To altered ♂♂
a	colour: white feathers to give mottled effect	whole plumage	54.5 increase	38.0* decrease
b	colour: green feathers added to give mottled effect	hackles	17.8 increase	0.0 unchanged
c	colour/contour: white feathers added, rachis outwards	hackles and crest	38.8 decrease	28.3 decrease
d	colour/contour: blue feathers added rachis outwards	breast, back, upper saddle	12.5 increase	18.4 decrease
e	colour: black dye applied	wings, back, saddle, hackles	0.0 unchanged	42.3*** decrease
f	colour: white feathers added producing a mottle	breast, abdomen	75.0 increase	23.5*** decrease

feathers in reducing solicitation may be indicative of the importance of White Leghorn plumage "colour" in sexual isolation. The importance of hackle and crest colour and contour cannot be entirely disregarded on the basis of the present results, since discriminations based on overall patterns may not be significantly disrupted by modification of single, small, feather zones. A modification similar to that in test a, which involved the addition of brown feathers in an all-over mottle, was carried out with RC males. However, no significant effect on RC female solicitation behaviour was observed.

Despite the cursory nature of this experiment, it was clear that the Brown Leghorn cock's dimorphic plumage colour pattern can be an important stimulus for breed-discrimination by females. It is interesting that the modification effected in test a reduced crouching to a significant degree, since modified males closely resembled White (Brown Leghorn) line cocks, which have an all-over white plumage mottle. Thus comparatively slight differences in plumage colouration between lines of one breed may have isolating value.

ii) The importance of bodily size of males:-

Strain distinctness in body size is marked in the present material. Testing its isolating value experimentally is difficult. One observation alluded to earlier is relevant in this connection however. An experiment involving the presentation of six large and six dwarf line Crossbred males to two female flocks, one B line and one RC line, was outlined

in Chapter II (see page 26). The two male groups were equated for plumage colour and comb type as far as possible. Dwarf line males resemble Leghorn males in size and height much more closely than do large line cocks. Dimensions of Leghorn and CBRD and MCBR males are given below:-

Male/Line	Mean Shank Length (Height)	Mean Body weight (Size)
Brown Leghorn	6.1 cms.	1.8 - 1.9 kgs.
White Leghorn	5.65 cms.	
CBRD	5.5 cms.	2.10 kgs.
MCBR	6.73 cms.	4.28 kgs.

As previously reported, females did not discriminate significantly between the two lines of Crossbreeds ($p > .05$), and copulation did not occur. The result is included here merely to indicate that size is not of paramount importance in 'rejection' of Crossbred males by Leghorn hens.

iii) The importance of male courtship vocalisations:-

A variety of male vocalisations occur during courtship of females. They can be divided broadly into two categories, display-specific and non-specific. The former category comprises the "titbit" call and the "stamp-squat" call, both of which are invariably associated with the displays from which they derive their names. The titbit call is slightly more flexible in this respect than the stamp-squat call, which I have never heard other than in association with stamp—squatting.

The tibbit call occasionally occurs during stamp-squat, perhaps because there is some postural facilitation involved. Non-specific calls are those not associated with particular displays, though they are sometimes observed in conjunction with one of several different non-vocal displays e.g. waltzing. These non-specific calls have never been extensively analysed (Wood-Gush, 1955).

Strain distinctness in male courtship vocalisation is in such qualities as pitch, tone etc., rather than in basic form which is similar throughout the sub-species. Pitch, for example, seems to be correlated with size in the present material.

Unfortunately, adequate facilities for tape-recording and playback of vocalisations were not available. Accordingly, an experiment involving modification of female hearing was carried out to test the significance of differences in vocalisation in sexual isolation between breeds and strains. Two small flocks of sexually-experienced B strain hens were tested under alternate-presentation conditions with five MCBR, five B, four R and four W line males, each male being presented twice per flock, with a fifteen minute presentation duration. Subsequently the females of one flock were deafened by tympanal ablation under anaesthesia (sodium pentobarbitone), the other flock acted as a 'dummy'-operated (anaesthesia only) control. Pre- and post-surgery auditory accuity test results indicated that surgical procedure had effected total deafness

in operates,controls remaining unaffected. Sound conduction via cranial bones is presumably negligible in the chicken. Social relationships amongst operates were unaltered. No recovery of auditory accuity was observed before the operates were killed some weeks later, and for short-term tests of this nature, the present deafening technique appeared to be as effective as more elaborate ones (Schwartzkopff, 1949; Schleidt, 1961 and 1964; Konishi, 1963). Forty-eight hours post-surgery the repitition of male presentation tests commenced. One operate female was excluded during retest because it contracted gout!

Figure 12 summarises the results. The high sexual isolation index between B hens and males of other strains was not significantly affected in either operates or controls (p in both cases $> .05$) and remained significant at the 1% level. Clearly discrimination can occur in the absence of vocal stimuli, which cannot be of paramount importance in the discrimination process. Vocal cues could be of some significance to sexually-naive females however, and the problem merits further attention. The level of solicitation of own-strain males by operates was not significantly reduced on retesting. The significance of this finding could be interpreted in one of three ways as follows:-

a) Courtship vocalisations have no signal function.

b) Courtship vocalisations, whilst having signal function, do not exert any affect on female <u>crouching</u> behaviour.

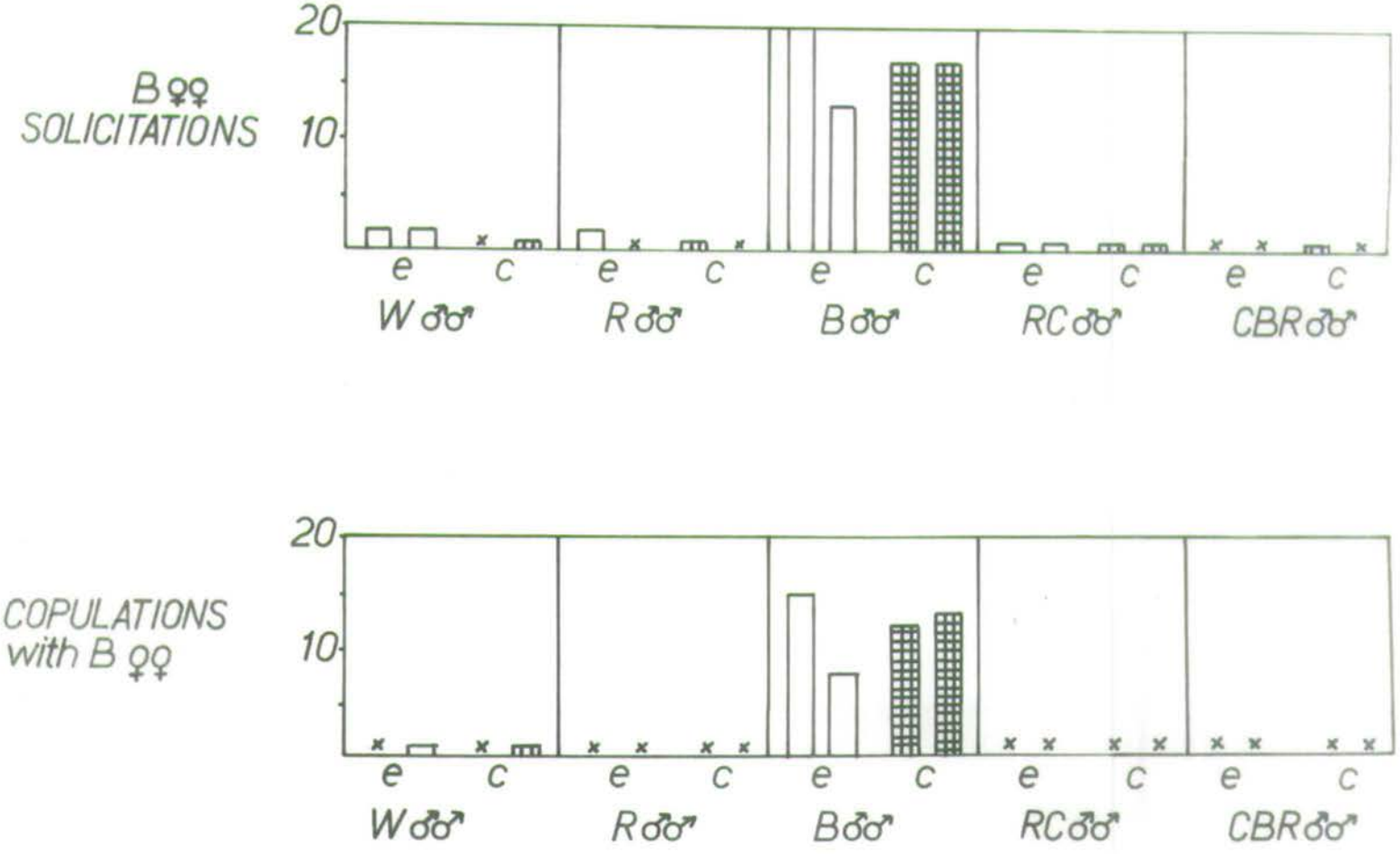

B♀♀
SOLICITATIONS
20
10
e c e c e c e c e c
W♂♂ R♂♂ B♂♂ RC♂♂ CBR♂♂
COPULATIONS
with B♀♀
20
10
e c e c e c e c e c
W♂♂ R♂♂ B♂♂ RC♂♂ CBR♂♂

Figure 12: The effect of deafening on homogamy in Brown Leghorn females

In each frame the two left hand columns (labelled e) refer to operated birds, the two right hand ones to controls. The left column of each column pair indicates pre-test results, the right column results after deafening. Crosses indicate zero readings.

W = W (Brown Leghorn) strain

R = R (" ") "

B = B (" ") "

RC = Reaseheath C (White Leghorn) strain

CBR = Crossbred strain

c) Courtship calls are only one of several stimuli evoking crouching in females, and in their absence other stimuli are sufficient to elicit the response.

It seems likely that the third explanation is true, since qualitative observations suggest that such calls certainly do have signal value and results presented later indicate that calls often preceed crouching of hens. A final decision must await further experimentation.

iv) The importance of male behaviour:-

Qualitative strain distinctness in courtship of males is slight. Quantitative strain differences in male courtship exist and their isolating value has been investigated. In two tests of female sexual behaviour with males of different breeds and strains (chapter II, pages 25 to 37), male courtship was measured quantitatively, and an attempt to analyse breed and strain differences and study their relationship to the observed female solicitation distribution was made.

Test 1 (page 25):-

The details of female solicitation have already been given in the text and figures 3 and 4. The present findings should be read with those details in mind.

Hatch a:-

Table 3 summarises the courtship of all male groups with Brown Leghorn females, the only females which discriminated significantly between breeds and exhibited homogamy. Quantitative variance in some aspects of courtship was observed.

TABLE 3

Test 1, Hatch a: Courtship of B line hens by males of three 'breeds'

Male Group	Total displays	Waltz	Wing flap	Titbit	Body shake	Head shake	Auto-preen	Tail wag	Bill wipe	Stamp + squat	Calls	High step	Rear apph.	Stru
B	919	162	82	282	25	145	31	1	16	3	139	11	19	2
RC	948	227	108	182	61	141	31	0	6	0	219	37	4	-[1]
CBR	1097	130	125	272	25	65	2	0	2	-[1]	398	8	2	-[1]

[1] This activity has never been observed in present material of this strain.

Overall variance in non-specific vocalisation was observed ($p < .01$), but was not correlated with female crouch distribution. Stamp-squat display has never been observed in Crossbred males in many hundreds of hours of observations; it is extremely rare in White Leghorn males, where I have only observed it once in a sexual situation at a very low intensity. Strutting has also never been seen in the present Crossbred or White Leghorn material. Such differences are in all probability ones of a threshold nature. Brown Leghorn cocks exhibited less non-specific vocalisation than other groups, but any functional significance of this finding remains obscure. Variance in male group courtship of Brown Leghorn hens was not correlated with distribution of female crouching, and was not important in establishing non-random crouching.

Hatch b:-

Table 4 summarises the courtship of the females of the three breeds by males. Some quantitative variance in male group display was observed, but was uncorrelated with the solicitation distribution in most cases and almost entirely due to the differential manner in which females responded to the different male groups. Despite the high level of stamp-squatting listed for Brown Leghorn group, breed variance in this display category was non-significant, as almost all of the observed occurrences of this display were attributable to one male. This male was not particularly 'successful' in eliciting crouching. White Leghorn males waltzed significantly more

TABLE 4

Test 1, Hatch b: Courtship of hens of three lines by males of each line

Male Group	Total displays	Waltz	Wing flap	Titbit	Body shake	Auto-preen	Tail wag	Bill wipe	Stamp + squat	Calls	High step	Rear apph.	Strutting	
B	1143	255	154	236	15	5	4	11	27[2]	374	0	6	5	To B ♀♀
RC	184	14	15	32	10	5	0	4	0	68	0	0	-[1]	
CBR	1175	113	226	232	27	8	0	00	-[1]	502	0	0	-[1]	
B	549	27	91	172	20	10	6	34	0	37	3	0	8	To RC ♀♀
RC	1623	296	113	583	73	12	1	21	1	561	2	0	-[1]	
CBR	1292	81	403	367	38	22	0	0	-[1]	266	2	0	-[1]	
B	956	270	82	208	9	16	6	15	16	229	4	0	5	To CBR ♀♀
RC	49	4	0	1	1	4	0	0	0	36	0	0	-[1]	
CBR	1287	144	174	314	21	8	0	0	-[1]	605	1	0	-[1]	

[1] These displays have <u>never</u> been seen in present material of this strain

[2] Performed mostly by one cock.

to White Leghorn hens than other male groups ($p < .01$), and were solicited significantly more than other males by them. Waltzing has a strong signal function, and is one of the main crouch-evoking displays (see page 162). However, it is entirely possible that the lower waltzing rate of the other male breed groups was due to the tendency of White Leghorn hens to avoid them.

As in Hatch $_a$, quantitative variance in male group display did not entirely account for the observed female solicitation distribution. Observations reported earlier (page 29) suggested that morphological differences between male groups were of importance in this respect.

Test A (page 34):-

The solicitation of B, R, and W line males by B line females was summarised in figure 5 and on page 35.
The mean rate and form of courtship of B line females by the three male line groups is illustrated in table 5. Inter-strain variance was observed in titbitting; mean titbit duration and female solicitation were negatively correlated ($p < .05$). W and R line males titbitted significantly longer on average than B line males, but did not differ from each other in this respect. Most of this titbitting was of low intensity type, having little signal value; it is thought to be a 'displacement activity', and may well have resulted in this case from of the sexual tendency of W & R males through their being "rejected" by the females. B line cocks had a significantly

TABLE 5

Test 1: Mean rate and form of courtship display to B line hens by males of three Brown Leghorn lines

Line	Waltz	Wing flap	Titbit	Body shake	Head shake	Auto-preen	Tail wag	Bill wipe	Stamp + squat	Rear approach	High step	Strut	Calls	Mean displays
B	12	11	14	1	6	0	0	1	1	4	2	0	22	82
R	3	32	14	1	4	0	0	0	0	0	1	0	8	57
W	3	1	26	1	4	0	1	0	0	0	1	0	0	44

higher mean display rate than and vocalised significantly more than W line males, but not than R line males. R and W line males were not solicited significantly differently by the females, and so such display differences seem of limited significance.

The results of both statistical analyses indicated that the effect on female solicitation distribution of quantitative differences in male display was either slight or too subtle to be detected by the measures taken. Similar analyses in other similar experiments gave essentially the same results i.e. a lack of correlation between quantitative variance in male courtship and female solicitation distribution.

The importance of other, qualitative strain behaviour differences (e.g. in posture, deportment, general activity) was not tested. Armstrong (1947) was of the opinion that deportment is one of the main cues in individual recognition in birds. Guhl and Ortman (1953) state that deportment per se can evoke either aggressive or submissive behaviour in other chickens; they found that the deportment of birds entering a strange physical environment was altered, and that resident birds apparently detected the change. It is not known whether a strange social environment also exerts this affect, but if such were the case, in the present inter-breed alternate-presentation tests, genetically-determined male group deportment differences would probably be enhanced. Qualitative strain differences in behaviour cannot be disregarded in the discrimination context,

and this aspect of the problem deserves further study.

It was noted earlier (page 35) that S (White Leghorn) line hens discriminated strongly between own-strain and R^C males which are identically "coloured". Differences in courtship did not account for the discrimination. Despite the overall evidence suggesting that male plumage colour and courtship behaviour are the main stimuli in breed and strain discrimination by female chickens, it is clear that in the absence of such stimuli, discrimination is still marked. Other stimuli, which the present study has not revealed, are clearly involved. Female discrimination is complex; this study of the stimuli involved does not give any indication as to the role of learning in the process.

Factors affecting discrimination by males:

In Chapter II, it was concluded that in simultaneous-presentation situations with living, cue females, males of normal experience discriminated between breeds but not between two highly similar strains within one breed. The present series of experiments was undertaken to clarify certain impressions gained as to the stimuli involved in male discriminations described in that chapter. In particular, the following three questions seemed pertinent:-

I) Is cue female plumage colour the main or only stimulus in breed discrimination by males?

II) Does cue colour disparity invariably enhance breed discrimination?

III) Were the biases shown by Brown Leghorn and Crossbred males in double-heterogamic tests due to the greater stimulus valency of the "preferred" breed, or to the tendency to avoid White Leghorn cues? If the former is true, what is the basis of the enhanced stimulus valency of the "preferred" breeds?

Material and Methods:

A cue animal modification technique was adopted, using the simultaneous-presentation situation already described. Eight RC and sixteen B adult cocks were used. The RC and B males were of normal experience. A ten-minute test duration was employed, and the usual simultaneous-presentation testing precautions and measures were taken. Modifications were of cue female plumage colour, and were effected by application of feather dyes and stains. Unmodified controls were used in such tests. After preliminary testing of males with normal cues, modification of one cue strain was carried out; subsequent retesting was similar to pretesting. In one test, number X4, modification of one cue bird took place before the test commenced, and a comparison of discrimination by B line males between a buff-coloured Crossbred cue and normal and black-dyed RC cues was made.

In a second series of tests, twelve ACBR (Crossbred) males were tested in a simultaneous-presentation situation on discriminations between i) variously coloured own-strain and S and B cue females and ii) S and B female cues. These males had been reared with female siblings to six weeks post-hatching,

kept in an isolated all-male flock to twelve weeks, and then caged individually in such a way as to be deprived of hetero-sexual experience, but not of visual experience of each other and S and B line males. Usual testing precautions and measures were taken, testing commencing when the males were twenty-four weeks old. The test duration was of the same order as in modification tests referred to above.

Results:

Modification experiments:-

Table 6 indicates the affects of modifications on male discriminations. The dramatic result of test XI indicates the extreme importance of plumage colouration in the breed discrimination process of White Leghorns. It has already been pointed out that Reaseheath C line males did not distinguish overtly between like-coloured strains within the White Leghorn breed. Cue colour disparity enhanced overt discrimination in White Leghorn cocks.

Tests X2 and X3 revealed the comparative insignificance of plumage colour as a stimulus in breed discrimination by Brown Leghorn males, and consequently of cue female colour disparity as an enchancer of discrimination. The result of test X4 revealed a bias in the courtship of Brown Leghorn males towards Crossbred cues that was clearly based upon stimuli other than plumage colour. Thus Crossbred females appeared to have a genuinely greater stimulus valency than White Leghorn females for Brown Leghorn males. However, the

TABLE 6

Effects of modifying cue female plumage colour on strain discrimination by males in simultaneous-presentation situation

Test no	Strain/ males	Discrimination	Modification of cue oo ++	Bias of courtship of modifieds		Bias of courtship of controls	
				Pre modification	Post modification	1st Test	2nd Test
X1	RC	B:RC	RC dyed black	W:RC *** TD:RC *** T:RC ***	NS NS NS	NS ** RC	NS *** RC
X2	B	B:RC	B dyed dark grey	W:B *** TD:B *** T:B ***	B *** B *** B	B *** B *** B	B *** B *** B
X3	B	B:RC	RC dyed black	W:B *** TD:B *** T:B ***	B *** NS *** B	B *** B *** B	B *** B *** B
X4	B	ACBR(buff) :RC	undyed and black-dyed RC cues utilised	W:NS * TD:ACBR *** T:ACBR		ACBR *** ACBR NS	

W = Waltzes in cage area
TD = Total displays in cage area
T = Time duration " " "
NS = Not significantly biased

* 5%)
** 2%) levels of significance in t test.
*** 1%)

slightly less significant discrimination in black-dyed RC/buff-coloured ACBR than in normal RC/buff-coloured ACBR tests may be attributable to either the enhancement phenomenon (though this seems unlikely since colour was unimportant in this and other discriminations by Brown Leghorn cocks) or to fleeing tendencies elicited by the white plumage of normal cue RC females. One additional finding is of relevance in this connection. In the original tests of male discrimination (table 1 and figure 10), it was pointed out that B strain males of Hatch b discriminated between ACBR and B cue females. In this particular test, white, brown and grey ACBR cues were paired with B cues, and the overall bias of courtship of B line males was towards ownstrain cues. However, an analysis of the male discriminations in each of the three separate tests with differently coloured ACBR cues, revealed that only when a white cue ACBR female was pairdd with a B cue female did males discriminate significantly in favour of the B cue. Indeed, the grey Crossbred cue elicited significantly more waltzing than the own-strain cue ($p < .01$) in B line males. Non-white Crossbred cues apparently have equivalent stimulus valency to B line cues for B line males, though to what extent this is dependent upon plumage colouration remains obscure. Possibly the large size of Crossbred females renders them supernormal stimuli, and this effect overrides colour disparity except when white is involved. It seems likely that the white plumage of the white ACBR cue elicited avoidance and "fear" in B males,

resulting in a significant bias of courtship towards the B cue.

That white plumage elicits fleeing and avoidance tendencies in non-white chickens was very apparent in the above-mentioned tests. B line males were seen to flee rapidly from white cues they had 'tentatively' approached, especially if the cue female moved. This type of response was never seen to non-white cues. Immelman (1959) observed a similar phenomenon in Australian Zebra Finches, and attributed it in his material to the lack of species-specific markings of the white mutant forms. Fisher and Hale (1956) report a similar phenomenon in their experiments on chickens.

Tests of Crossbred males:-

The results are presented in figure 13. The early experience of these twelve cocks differed from that of males alluded to in the previous section, and did not allow of analysis of the mode of discrimination exercised by normal-reared males; nevertheless, the present tests did shed some light on the stimuli involved in male discriminations, and it is for this reason that they are included here.

The failure to discriminate in the white ACBR/S test indicated that plumage colour was probably one of the stimuli involved, since both cues were all-white. The results were explicable on the basis of differential stimulus valencies of plumage colours, such that stimulus valency decreased in the colour series:- Grey = Light Brown > White > Dark Brown. However, no true enhancement was observed, and white plumage

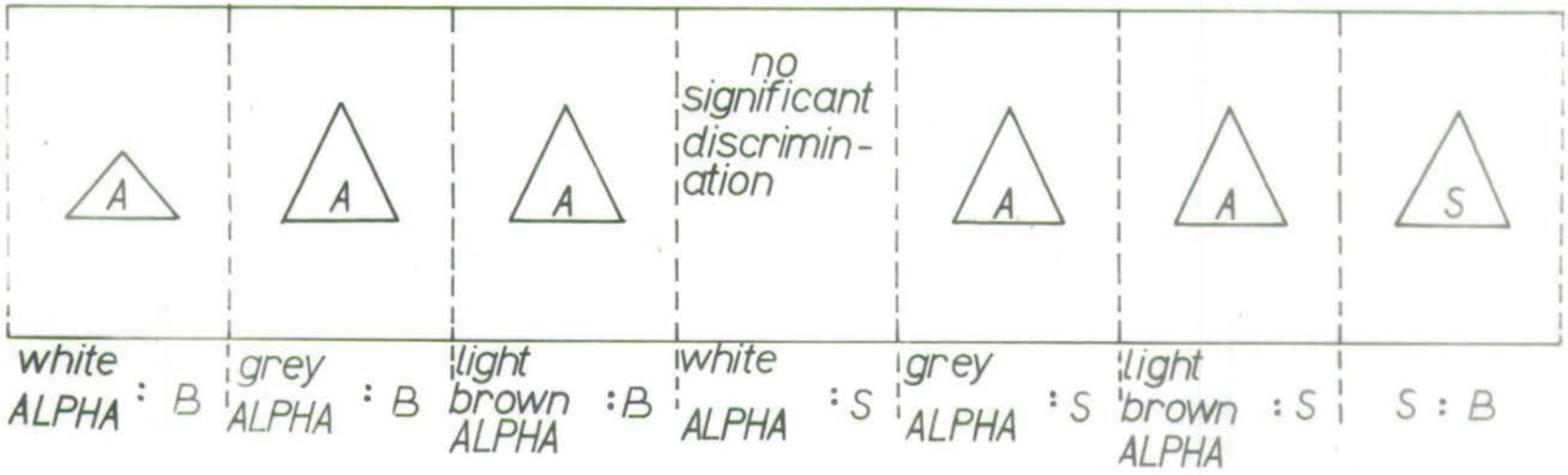

A
A
A
no significant discrimin-ation
A
A
S
white ALPHA : B
grey ALPHA : B
light brown ALPHA : B
white ALPHA : S
grey ALPHA : S
light brown ALPHA : S
S : B

Figure 13: Discrimination between females of different breeds in a simultaneous-presentation situation by sexually-naive Crossbred males

Nature of discrimination test indicated at base of figure. Criterion of significant difference in courtship of cue females taken as 5% level of confidence (t test). "Preferred" strain indicated in triangle, and significance of "preference" beyond 5% level directly proportioned to triangle size (all measures combined)

A and ALPHA indicates - ACBR strain

S indicates - S(White Leghorn) strain

B indicates - B(Brown Leghorn) strain

did not elicit any fleeing or avoidance in males. Moreover the difference in discrimination significance level between the White ACBR/B and S/B tests is difficult to account for by the colour series explanation. The differences in discrimination between normal-reared and sexually-naive Crossbreed males will be discussed later. It is of interest to note that despite the enormous individual differences in Crossbred male plumage colour, all such males discriminated in a similar manner, showing a bias in courtship behaviour towards own-strain hens of all colours which were paired with Brown Leghorn hens, and towards all own-strain hens except white ones that were paired with White Leghorn hens. It thus seemed probable that other stimuli besides plumage colour were involved in breed discrimination by these males.

Conclusions

Despite the uncomprehensive nature of the present study, it has shown that the expectation that the phenotypic characteristic which differs most between breeds and strains, namely plumage colouration, would form an important cue in the discrimination process was essentially correct. To some extent both sexes appear to use this character as a cue in discrimination, and in this respect, chickens behave like many other bird species. In wild birds, species-specificity in plumage, vocalisation and courtship display possesses the greatest isolating value, whereas in the Fowl, in which behavioural and vocal divergence is less marked than that of

plumage colour, it is not surprising that this latter character is most important in the discrimination mechanism.

Sibley (1957 and 1959) has argued that reinforcement of isolating mechanisms in birds utilizing visual and vocal courtship signals enhances the species "recognition" characters, usually male dimorphic plumage and behaviour patterns. Enhancement is additionally increased in polygamous species exhibiting a marked degree of sexual selection (see also Huxley, 1945). Since it appears likely that the Junglefowl conform to this latter definition to some extent (Hume, cited in Beebe, 1918), it is reasonable to suppose potential ethological isolating mechanisms would be well developed between the four species, even in the absence of actual reinforcement under syntopy. (The distribution of the four species as demonstrated in Hutt, 1949, shows that syntopy may well have existed between some of them at some stage(s) in the geological past). It is thus interesting to find that in Brown Leghorns, a breed phenotypically resembling Gallus bankiva closely, and often considered a 'wild-type' chicken, male dimorphic plumage pattern is an important stimulus in breed discrimination by females. It is perhaps not unrealistic to speculate that the high sexual isolation index of the Brown Leghorn has been "inherited" in a largely unaltered form from its supposed ancestral progenitor.

Moreover, it appears that artificial selection of breeds and strains of Fowl of markedly differing plumage hue has produced potential sexual isolation between such groups.

What is especially interesting in this connection, is what reduction of male plumage colour patterning in many breeds has done to the discrimination mechanism. In the present work, I have not thoroughly investigated the cues involved in discrimination by females of such a breed. However, in White Leghorns, selection for mono-coloured plumage appears to have somewhat simplified the discrimination process of males, rendering the overall whiteness of plumage the critical stimulus, and others unimportant. Females utilise other cues in a situation permitting of sexual behaviour on the part of both sexes. It is clearly too early to speculate further along these lines, and objective judgement must await further experimental evidence. In particular it is of interest to know whether characters (e.g. minor morphological and behavioural differences) which have little isolating value in wild species have acquired such value at the strain level in the Fowl.

Present results underline the complexity of discrimination in the Domestic Fowl. That the features of the head region are not particularly important in breed discrimination by hens is complementary to the findings of other workers (see Thorpe, 1951; Guhl and Ortman, 1953: Immelman, 1959), who noted that such features are more important in individual "recognition". There is some evidence that head region characters are more important in discrimination of sex in the Fowl (see Chapter VI). It is not clear whether the

three breeds used in this experimental series discriminate in exactly the same manner. There is some evidence to suggest that Crossbred females, by virtue of their size, may act as supernormal stimuli (Tinbergen, 1951) to Leghorn males. This could account for the reduced levels of own-breed bias in courtship behaviour exhibited by males of these breeds in tests involving homogamic and Crossbred cue females. The lack of breed-specific plumage markings may enhance the stimulus value of Crossbred females. Morris (1956) observed inter-specific clumping behaviour between Doves and Java Sparrows. The 'fluffed' posture adopted by the former overcame species differences in markings, and its comparatively immense size rendered it a supernormal stimulus for clumping to the Sparrows.

Although Crossbred females really have a stronger stimulus valency for courtship behaviour in Brown Leghorn males than White Leghorn females, white plumage appeared to have an inhibitory effect on courtship in the Brown Leghorn cock, and enhance the courtship bias. However, the results for Crossbred males were not entirely explicable on the same basis. The difference in discrimination between the Crossbred males described here and those discussed in Chapter II may be a result of their different early experience, though within and between hatch variability in morphological characters could be involved in addition. The stimuli involved in homogamy of Crossbred cocks are far from clear at the present

time.

As I have already pointed out, the observed inhibitory affect of white plumage on sexual behaviour of non-white birds is reminiscent of other workers' findings. In the present work, the affect was most pronounced on Brown Leghorns, but could not be attributed entirely to a lack of markings in white individuals, since Crossbred birds would also have produced alarm reactions and inhibitory affects if this were so. Whiteness *per se* appears to have specific alarm-inducing properties for non-white birds. Other data substantiate this finding (Lill, unpublished).

In a later chapter, it will be demonstrated that the waltz display possesses strong signal function, being one of the main solicitation-eliciting displays, in Brown Leghorns. The present results indicate the isolating value of the plumage colour patterning of the Brown Leghorn cock. It is not insignificant that the dorsal colour pattern of blacks, browns and chestnuts is particularly well displayed during waltzing, when the lateral orientation of the male, tilting of the body towards the female, and raising of the contralateral feathers render it more conspicuous than in other courtship activities.

Previous studies of breed-discrimination in Fowls have pertained to mixed-breed flocks mostly; comparison with present results is therefore tenuous. But it should be recorded that Hale (1957) also found that colour played some role in overt breed discrimination, though other stimuli were

also utilised in open-pen situations. Breed and strain discrimination is, of course, a more persistent phenomenon than individual "recognition". The latter breaks down after approximately two-three weeks of contactual isolation (Schelderup-Ebbe, 1923; Maier, 1962).

The results presented above show, albeit in a domesticated species, that genetic divergence of "populations" in relatively few characters may be sufficient to effect a considerable level of reproductive isolation. In the light of the present findings, it is perhaps not difficult to visualise the type of assortative mating described by O'Donald between plumage colour phases of the Arctic Skua differing little in behavioural characteristics, or by Cooch and Beardmore between colour types of the Blue-Snow goose, 'assisting' in significant splitting of populations, though it seems unlikely that such behaviour could effect splitting per se.

CHAPTER IV

The affects of experience on homogamy in the Fowl

It is really a truism to state that in wild avian and other species, orientation of adult sexual behaviour is generally intra-specific, interspecific mating and hybridisation being comparatively rare. Following the description of the imprinting phenomenon by Heinroth and Lorenz, ethologists have devoted much attention to elucidating the factors governing the orientation of adult sexual responses. One of the most controversial problems has been the role of reinforcing experience in enhancing the affects of Sexual Imprinting as an orientating mechanism in precocial birds. In altricial species there are very few examples of imprinting-like processes; in such species, and particularly in brood-parasitic ones (Hamilton and Orians, 1965) orientation may be differently regulated, possibly on an innate basis. Klopfer (1962) points out that even in nidicolous species, learning of species characteristics must occur at the comparatively restricted nestling stage.

Even amongst precocial species of bird, sexual imprinting is not the only factor involved in orientation, or the only mechanism of species discrimination (Fabricius, 1962). Recent research points more and more the intra-specific orientation of sexual responses being dependent upon the release of innate responses and learning. Schutz (1965) has shown that in the Mallard (Anas platyrynchos), males imprint sexually, but

also exhibit an innate tendency to pair with conspecifics. Females do not usually imprint, responding innately to male nuptial plumage releasers. In a non-dimorphic species, females did however imprint sexually. Gottlieb (1965) reports a similar innate tendency to respond 'preferentially' to specific vocalisations in ducklings and chicks, which was highly resistant to change by learning. He argues that such a tendency will reduce the likelihood of sexual imprinting to visual characters of other species.

It is not clear whether imprinting to siblings, a phenomenon demonstrated by Guiton (1959) and Taylor and Sluckin (1964) in domestic chicks and Fabricius in ducklings (1957), normally affects subsequent adult sexual behaviour orientation. Guiton's findings suggest that it may in fact weaken fixation on a parent-surrogate (human being), but, on the other hand, it is entirely possible that by keeping juveniles in close contact, especially at the time of ontogeny of sexual behaviour, it could reinforce other factors regulating the intra-specific orientation of subsequent adult sexual behaviour. Moreover, chicks poorly mother-imprinted may follow chicks well mother-imprinted, reinforcing the affects of sexual imprinting. Many primary functions have been theoretically ascribed to sib imprinting (Gray, 1961; Taylor and Sluckin, 1964). Although sib imprinting is apparently more difficult to achieve experimentally than classical imprinting (Schutz, 1965), its role as an orientating mechanism for sexual behaviour deserves

further investigation. The regulation of the two processes is by the same mechanisms and stimuli (Fabricius, 1962).

The restriction of sexual imprinting to a brief, early, critical period can no longer be accepted (Hinde, 1962; Fabricius, loc. cit.). It is clear that experience or learning of a type which cannot really be labelled as imprinting can affect the orientation of adult sexual behaviour in many birds. Thus a consideration of the possible affects of social environment on sex behaviour orientation cannot exclude the possibility of experience at any juvenile stage being important. In summary, the orientation of adult sexual behaviour may be affected in a single species by both genetic, early and later experiential factors.

It has been pointed out earlier that homogamy occurs in the present material in the absence of any opportunity to imprint to a parent. It is pertinent in the present study to determine the relative importance of innate responses and experiential factors in effecting homogamy in the Fowl. As in Mallards (Schutz, loc. cit.), the male domestic fowl appears, as far as visual stimuli are concerned, to have an innate disposition to respond "preferentially" to conspecifics. Guiton (1962) found that cocks imprinted to humans "preferred" hens to humans in absolute terms. Also androgen-injected, seven-week old cockerels, which had been kept in total social isolation, reacted sexually to a stuffed, silent, model pullet. Wood-Gush (1958) observed that

deprivation of intra-specific visual experience until sexual maturity did not seriously affect cocks' mating "success" with hens, though deprived males did not mate successfully until they had been exposed to females for some time. Guiton (1962) pointed out that early intra-specific social experience did facilitate the development of sexual preference for conspecifics in the cock, by increasing stimulus specificity, enhancing sexual responsiveness, and leading to greater social integration. The overall picture emerges of an innate conspecific sexual preference in males which is facilitated and refined by conspecific heterosexual experience.

Similar analytical studies are lacking for the hen. It has already been reported that the female Brown Leghorn responds to the dimorphic plumage colour pattern of the male, and Schutz (loc. cit.) found that as a general rule in dimorphic duck species, females respond innately to the same type of stimuli. One of the present objectives of this study was to determine whether the same is true of the female chicken.

The importance of experience in overt breed and strain discrimination in chickens is unknown. Fisher and Hale (1957) observed own-breed biases in sexual behaviour in "choice" tests of New Hampshire males reared in all-male, single-breed flocks, with or without experience of females and other breeds from ten weeks old to sexual maturity. The possible affects of homosexuality were not analysed however.

McBride (1964) reared four strains communally from a) hatching and b) ten weeks old. Strain dominance occurred, agonistic reaction between was greater than that within strains, and early (ten week) segregation enhanced discrimination. Some of the experiments reported below are the first in a series designed to determine the relative importance of innate and experiential factors in homogamy in the chicken. The abolition of homogamy and its reversibility as a result of modifying the juvenile social environment have also been studied to some extent.

Under conditions of true syntopy in wild species, behavioural and visual "interaction" between the two species must be common. Ethological isolating mechanisms can be important in species maintenance under such conditions. The stability of such mechanisms is critical, particularly in conditions especially likely to promote weakening of sexual isolation (Sibley, 1959). There is some evidence to show that effective breakdown of sexual isolation can occur under certain conditions, particularly when the ratio of species individuals is disproportionate (Sibley and Short, 1959; Miller, 1955). In such circumstances, several phenomena may be seen. If hybridisation occurs and hybrids are at a selective disadvantage, the parental populations may be eliminated in time. As a result of hybridisation, introgression and swamping may develop, though introgressive hybridisation may be an important evolutionary mechanism on occasions, increasing

genetic variability. When sexual isolation breaks down but other barriers to effective hybridisation exist (Pettingill, 1959; Gudmusson, 1932), there is an effective reproductive energy wasteage and reduced effective population size of parental populations may result.

Experimental breakdown of ethological isolating mechanisms was noted by Haskins and Haskins (1950) in poeciliid fish. In the species studied, it was known that species discrimination, a visual process, was partly innately and partly experientally determined. Where species discrimination is entirely innate, inter-specific mating is likely to occur only under conditions of extreme sexual motivation, in which a sub-optimal releaser releases sexual behaviour due to an abnormally low receptivity threshold. Such was apparently the case in the experimental breakdown of sexual isolation seen in some moths (Standfuss, 1896) and tsetse flies (Vanderplank, 1948).

Some of the experiments described below were designed to test the stability of homogamy in chickens which were known to exhibit this trait as adults when tested in a "choice" situation. It was also hoped that the affects on homogamy of modifying adult social environment would shed further light on the normal affects of juvenile experience on homogamy. It should be pointed out that this aspect of the present study of non-random mating in chickens, that is the importance of experience in homogamy, is only in its early stages; experiments involving analysis of the affects of juvenile

environment on adult behaviour are necessarily protracted in a slowly-maturing species. In consequence, some of the data here presented are based on limited samples, most experiments have not been repeated and one experiment lacked an adequate control. The data are included however, in order to give a comprehensive view of the problem, and to serve as a framework for future study. Further experiments currently being undertaken will be outlined later.

The affects of social environment on homogamy in adult males

I. Affects of Juvenile social environment

Material and Methods:

Experiments have involved males of the B, Alpha Crossbred and RC lines. Males were reared under different juvenile social environmental regimes, and subsequently tested as adults on discriminations between females of differing breeds in a simultaneous-presentation situation of the type already described. Tests were similar to those described in chapter II, the same techniques, precautions and measures being adopted. Three modifications of the normal (own-strain, heterosexual) type of juvenile social environment were undertaken on three separate groups of experimental subjects as follows:-

Test A:

Two groups of eleven Brown Leghorn (B line)males were reared separately from hatching. A control group was reared under normal, (own-strain heterosexual) juvenile, social

environmental conditions until twenty-three weeks post-hatch, when males were removed from the flock and caged individually prior to testing. The second group of males was reared as an all-male, visually-isolated flock until twenty-three weeks and thereafter during testing. All males were then tested singly on discriminations between live cue females as follows:-

a. Alpha Crossbreed (white, brown and grey plumage types)/B

b. Alpha Crossbreed (brown and grey plumage types)/S

c. B/S

Test B:

Twelve Alpha Crossbred males were reared from hatch to approximately six weeks in a normal juvenile social environment. From six to twelve weeks they were kept in an all-male, visually-isolated flock, and subsequently caged individually in sight of one another and of S and B males, but in isolation from females. They were maintained in this condition until twenty-four weeks when testing commenced, and during testing. Simultaneous-presentation tests involved the discrimination between live hen cues as follows:-

a. Alpha Crossbreed (white, grey and brown plumage types)/B

b. Alpha Crossbreed (white, grey and brown plumage types)/S

c. B/S

The results of this test have been described in another context earlier (see chapter III).

Test C:

Control males, six B line, six Crossbreed, and six RC line, were reared in normal own-breed flocks, visually isolated from all other birds from two weeks after hatching. Of these, the Crossbred and RC males had a little sexual experience of other breeds after sexual maturity and prior to testing. Five B, two RC and four Crossbred males (experimentals) were reared from two weeks to sexual maturity in a visually-isolated, heterosexual, tri-breed flock representing all the breeds involved in the experiment. All males were removed from rearing flocks when fifty per cent of the hens were in lay, and caged individually in a battery room containing only males. Testing commenced a few weeks later, the live cue hens being presented in pairs to the individual males as follows:-

a. Crossbreed (two dark coloured plumage types)/B

b. Crossbreed (two dark coloured plumage types)/RC

c. B/RC

Disparity in male sample size between controls and experimentals was due to high juvenile mortality in the tri-breed flock in what was designed essentially as a pilot experiment.

Discriminations made by control groups in Tests A and C have been presented earlier as illustrations of discrimination by normal-reared males (see chapter II). All tests were carried out from 15.00. to 18.00. hours, and suitable intervals between tests were employed.

Results:

Test A:

Table 7 is a summary of findings. Control and experimental males exhibited overall own-breed biases in courtship in tests involving homogamic cues, and a bias towards Alpha Crossbreed cues in Crossbreed/S tests. There was only one major difference in discrimination between experimentals and controls. Experimental males generally exhibited slightly less strong biases than controls, particularly in waltzing.

Test B:

Results have already been given in figure 13 and on pages 62 to 66 . In all cases where cue colour disparity occurred, significant courtship biases were seen. Own-breed bias was seen in all but one test involving homogamic cues. Unfortunately no control was available, but it was clear that adult own-breed bias occurred in most cases when heterosexual, own-strain experience had been confined to an early ontogenetic stage (0 to 6 weeks after hatching).

Test C:

Results are presented in tabular form in table 8. It was evident that experience with other breeds during the juvenile phase reduced the level of discrimination in Brown Leghorn cocks, causing the disappearance of homogamy in the B/RC test. Tri-breed reared males displayed less intensely and frequently than controls. Own-breed bias was reduced in White Leghorn/

TABLE 7

Affects of modification of the juvenile social environment on homogamy in Brown Leghorn cocks: Test A

♂♂ Simultaneous-presentations of ♀♀

		CBR : B	Brown CBR : B	Grey CBR : B	White CBR : B	CBR : S	Brown CBR : S	Grey CBR : S	B : S
Controls	Waltz:	470 540*	137 157	254*** 142	79 241***	611**** 73	246*** 31	365*** 42	434*** 43
	Total Displays:	979 1494***	355 414	394 471	230 609***	1129**** 289	488*** 124	641*** 165	1086** 202
Experimentals	Waltz:	20 60***	8 22	7 4	5 34	6 0	0 1	6 0	21 1
	Total Displays:	318 441***	191 187	91 123**	36 131*	271**** 95	171** 54	100*** 41	243*** 75

* .05
** .02
*** .01
**** .001

} Levels of significance

TABLE 8

Test C: The affects of a mixed-breed juvenile social environment on homogamy in the domestic cock

MALES	EARLY EXPERIENCE		Simultaneous-presentations of ♂♂ ++					
			CBR : BR. LEGHORN		WH. LEGHORN : BR. LEGHORN		CBR : WH. LEGHORN	
Brown Leghorn (B)	Homogamic (controls)	Waltz	63	100*	1	132**	165**	1
		Total Display	214	380	73	454**	450**	37
		Secs. in Cage Area	1575	3447**	922	4571**	4536**	571
Brown Leghorn (B)	Homo + Heterogamic (experimentals)	Waltz	23	16	15	11	25	12
		Total Display	172	248	121	170	179	159
		Secs. in Cage Area	2615	1734**	1927	2818	2558	2422
White Leghorn (RC)	Homogamic (controls)	Waltz	11	1	30**	2	22	20
		Total Display	104	85	325**	36	147	261
		Secs. in Cage Area	1317	1581	4297*	376	1247	3526**

MALES	EARLY EXPERIENCE		Simultaneous-presentations of ♂♂ ♀♀					
			CBR : BR. LEGHORN		WH. LEGHORN : BR. LEGHORN		CBR : WH. LEGHORN	
White Leghorn (RC)	Homo + Heterogamic (experimentals)	Waltz	22	6	8	7	24**	0
		Total Display	87	56	88	35	106**	25
		Secs. in Cage Area	992	832	1211**	562	1187**	479
CBR strain (Alpha)	Homogamic (controls)	Waltz	63	43	20	65	101**	26
		Total Display	284	184	98	323**	450**	127
		Secs. in Cage Area	3131	1895	1195	3830**	4792**	1162
CBR strain (Alpha)	Homo + Heterogamic (experimentals)	Waltz	20	21	5	41	67*	5
		Total Display	109	207	103	231	219	128
		Secs. in Cage Area	905	2147**	832	1937	1674	1708

* 5%
** 1% levels of significance

Brown Leghorn tests of White Leghorn males reared in the mixed flock, as compared with control White Leghorns. In the Crossbred/White Leghorn test, experimental White Leghorn males failed, unlike their control counterparts, to exhibit homogamy; indeed they showed reversed bias (heterogamy). Juvenile experience in the tri-breed flock strongly affected discrimination. Crossbred cocks of mixed juvenile experience also differed in discrimination from controls, exhibiting a Brown Leghorn-bias in the B/Crossbred test, no preference in the RC/B test, and weakened homogamy in the Crossbred/RC test.

It was evident from present findings that after no or temporarily strongly restricted heterosexual, own-strain experience, males exhibited homogamy at a level only slightly less significant than that shown by normal-reared males. It was not entirely clear, however, whether homogamy had an entirely innate basis in cocks, since i) affects of homosexual experience (actual and visual) were not precluded in these experiments and ii) experience with 'own-body' may also affect sexual behaviour (Kruijt, 1964) and homogamy. Whether or not homogamy occurs in adult Brown Leghorn cocks as the total or partial result of juvenile experience, it was apparent that non-white Crossbred females were of roughly equivalent stimulus valency to Brown Leghorn females for such males, and that in this respect, own-breed bias was based on a response to relatively unspecific stimuli. The possibility that non-white Crossbred cues acted as supernormal female

stimuli cannot be disregarded in view of their large size. It is not possible to draw any firm conclusion as to the absolute importance of experience in homogamy in male chickens as yet, though if experience is normally involved, it must presumably be of a fairly unspecific nature.

Finally, the test results for males reared in the tri-breed flock indicate that homogamy can be modified by the juvenile social environment, even to the extent of total abolition. The social organisation of this flock during ontogeny was not known, and the relative importance of mixed experience and dominance relationships during development in affecting homogamy remains a matter of speculation.

II. Affects of Adult social environment

Material and Methods

Twenty-seven S and sixteen B line adult cocks were studied. All were of normal juvenile experience. The birds were divided into three main groups, one of fifteen S males, one of twelve S males, and the third of all sixteen B males. All birds of a groupswere first tested in a simultaneous-presentation situation of the type used throughout this study, in which they were confronted with live S and B female cues. The usual testing techniques and measures were used, tests being of nine minutes duration, and taking place on two successive days. Thereafter, each main group was divided into three or more subgroups, each of which was subjected to a different type of social environment for the following

fourteen days. At the end of this period, all males were returned to their individual home cages in the battery room of cocks. Replicate tests on the S/B discrimination were then carried out on the two following days. The types of social environment used in the present experiment and their application can be summarised as follows:-

Main Group I (twelve S males):

Subgroup a - Deprived environment (Controls). No experience of females, kept in home cages throughout.

Subgroup b - Homo-heterogamic heterosexual environment. One Brown Leghorn and one White Leghorn female placed in home cage on alternate days.

Subgroup c - Homo-heterogamic visual environment. Caged individually in pen containing equal numbers of Brown and White Leghorn females.

Main Group II (sixteen B males):

Subgroup d - Deprived environment (Controls). No experience of females, kept in home cages throughout.

Subgroup e - Homogamic visual environment. Caged individually in pen of homogamic females.

Subgroup f - Heterogamic visual environment. Caged individually in a pen of heterogamic females.

Subgroup g - Homo-heterogamic visual environment. Caged singly in a pen containing a homogamic male with free access to heterogamic females.

Main Group III (fifteen S males);

Subgroup h - Deprived environment (Controls). No experience of females, kept in home cages.

Subgroup i - Homogamic heterosexual environment. Penned or caged individually with homogamic females.

Subgroup j - Heterogamic heterosexual environment. Penned or caged individually with heterogamic females.

All subgroups of a Main Group were of similar size. Where males were caged with females, the female was changed frequently. During the fourteen day period, observations were made occasionally, and revealed that males were actively responding to females, even when occasionally the latter were avoiding them. Two males in Subgroup e contracted disease during the fourteen day period, and were not retested. Results for this Subgroup are therefore based solely on the two remaining cocks. Results were mostly analysed by the t test, the five per cent level of confidence being taken as the criterion of significance.

Results:

Table 9 and figure 14 summarise all results and indicate the significance levels of the observed discriminations. All subgroups exhibited significant homogamy during pre-testing, and in no control subgroup was the level of this response depressed on re-testing.

Main Group I:-

Neither type of experimental environment significantly

TABLE 9

Affects of various adult social environments on homogamy in the male domestic fowl

	Subgroup a		Subgroup b		Subgroup c				
	S cue	B cue	S cue	B cue	S cue	B cue	S cue	B cue	
W:	104	4	124	2	139	1			
TD:	171	17	194	19	221	18			
IO:	8	0	6	2	6	2			Main Group I
W:	156	12	123	1	99	0			
TD:	249	54	189	34	168	4			
IO:	8	0	8	0	8	0			
	Subgroup d		Subgroup e		Subgroup f		Subgroup g		
W:	4	41	6	72	9	71	4	44	
TD:	36	136	37	115	22	182	22	87	
IO:	2	6	0	4	0	8	1	7	Main Group II
W:	1	94	7	36	17	93	10	27	
TD:	31	163	20	99	29	180	22	69	
IO:	0	8	0	4	1	7	2	5	
	Subgroup h		Subgroup i		Subgroup j				
W:	106	16	179	2	189	11			
TD:	266	51	319	38	467	22			
T:	61.0	11.7	53.8	9.4	71.4	2.4			Main Group III
W:	114	9	211	0	158	94			
TD:	228	30	326	31	318	175			
T:	51.8	13.5	59.8	10.5	54.5	24.0			

W = Waltzes TD = Total Displays T = Time duration (minutes) IO = Initial Orientation

All birds tested on B/S discrimination. Upper portion of each set of data represents pre-test, lower represents re-test.

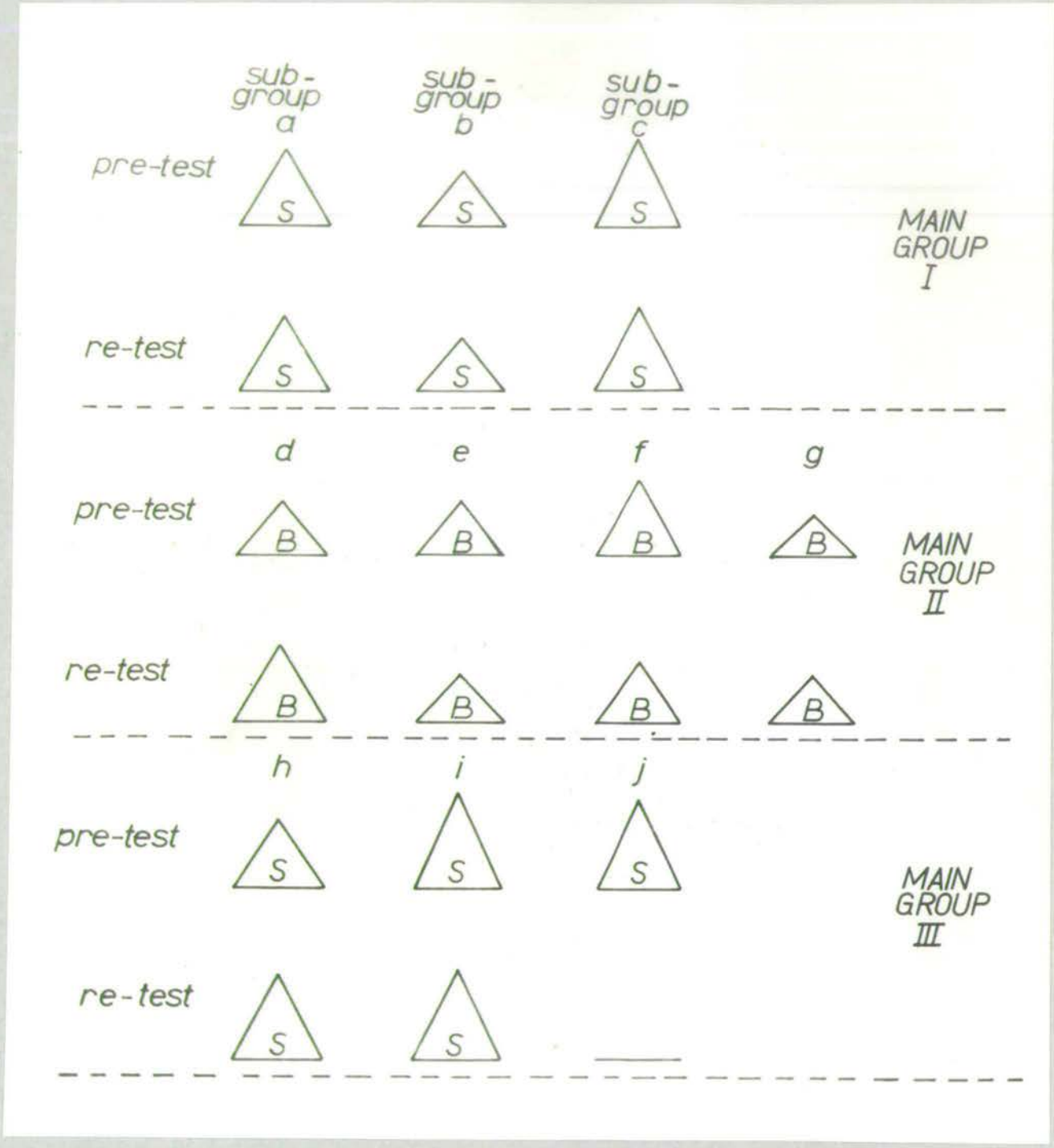

sub-group a
sub-group b
sub-group c
pre-test
S
S
S
MAIN GROUP I
re-test
S
S
S
d
e
f
g
pre-test
B
B
B
B
MAIN GROUP II
re-test
B
B
B
B
h
i
j
pre-test
S
S
S
MAIN GROUP III
re-test
S
S

Figure 14: Summary of data in table 9, indicating significance levels of observed discriminations

Direction of bias in courtship indicated in triangles. Triangles indicate significant bias at 5% level, and triangle size is proportional to degree of bias beyond 5% level (all measures combined)

S = S strain

B = B strain

affected homogamy. There was no real evidence of either satiation or reinforcement affects in the two experimental Subgroups b and c, either because visual and sexual experience did not affect homogamy once established, or because simultaneous experience of both strains had a mutually inhibiting affect.

Main Group II:-

Controls showed an enhanced level of homogamy on re-test, whereas Subgroups e and f showed some reduction in homogamy strength (though not to non-significance), and Subgroup g was little affected. The enhancement seen in the controls may reflect a normal fluctuation or be the result of deprivation; a similar phenomenon, though of a less pronounced character was seen in Main Group III controls. If reduction of the level of homogamy in Subgroups e and f was due to habituation (experience without reinforcement), it must be due to habituation to the female stimulus generally, rather than to females of a particular strain. There are, of course, further elaborations and interpretations of these findings which could be advanced, and clearly further experimentation is necessary. The overriding significance of the results remains, however, that homogamy was relatively unaffected by the social environmental modifications carried out, and that it has considerable stability.

Main Group III:-

Sexual experience with homogamic females did not alter homogamy significantly in males of Subgroup i. Although exposure to own-strain and Brown Leghorn hens may have produced some habituation or satiation in Sub-groups i and j, the total abolition of homogamy in the latter appeared to be due to a genuine breakdown of isolating mechanisms. Data for individual cocks in Subgroup j showed that only three males were significantly affected by the treatment. Only two of these exhibited heterogamy on re-test, the other failed to discriminate between the cues significantly. Nevertheless, the affect on these three males was sufficiently marked to reduce group discrimination level to non-significance. There was no indication that males significantly affected by the treatment were the weakest discriminators during pre-testing. Thus homogamy in S line males had some degree of stability, but was not an irreversible trait.

The Affects of Juvenile social environment on homogamy in adult females

Material and Methods:

Data to be presented below relate chiefly to one experiment in which two Brown Leghorn (B line) flocks were reared separately from hatch to sexual maturity in differing degrees of isolation from other birds. One flock consisted of fourteen females reared with seventeen males in complete visual and partial auditory isolation from all other birds in a ten foot

square run. These females were controls. All males were removed shortly prior to testing, which commenced at twenty-three weeks after hatching. The experimental flock, comprised of fifteen females, was raised in total visual and auditory isolation from all other birds for the same period.

Alternate-presentation tests of homogamy involved presentation singly, twice, for fifteen-minute periods, of six unfamiliar B, six S, and six Alpha Crossbred males. The usual measures and testing techniques were used. Testing extended to twenty-five weeks after hatching; a single B line male was then introduced into the experimental flock until thirty-four weeks post-hatch, and re-testing with five B and five S line males began at thirty-five weeks after hatching, and involved both flocks.

Results:

The level of sexual solicitation showed seasonal decline in controls in the second series of tests (thirty-five weeks), and so crouching intention movements were also scored. Several young S line cocks used in series II tests were aggressive to the Brown Leghorn females, and a serious statistical comparison of the results in the two test series was thus not feasible. Results are given in table 10, and can be summarised thus:-

Series I tests:

i) Control females solicited the male groups in a non-random manner ($p < .01$ in an analysis of variance), crouching

TABLE 10

males

Solicitation and solicitation intention movements of female flocks

	B line	S line	ACBR line	
1st Test Series (23rd week)	27	5	2	controls
	5	0	0	experimentals
2nd Test Series (35th week)	27	9	-	controls
	38	4	-	experimentals

Affects of juvenile social environment on homogamy in Brown Leghorn hens

significantly more to own-strain than S or Alpha males, between which they did not discriminate.

ii) Experimental hens did not crouch in a non-random manner. They solicited cocks very little, but all crouches and intention movements of crouching which were seen were in response to Brown Leghorn cocks.

iii) Control hens fled initially from S line cocks, but soon habituated to them. Experimental hens fled from all cocks in an alarmed manner, and though some habituation did occur later in the test series, it was far less marked than that of controls. Experimental hens did not respond to male 'approach-inducing' courtship displays, unlike controls. Male mounting attempts elicited rapid flight and "alarm" in experimentals but not in controls.

iv) Control hens were overtly aggressive to Alpha and B cocks, but experimental hens were not.

Series II tests:

i) A definite tendency to homogamy was observed in both controls and experimentals.

ii) None of the above-listed differences in other behavioural responses to males existed between the two female flocks.

Results indicated that pronounced homogamy did not occur in the absence of normal experience, showing that to some extent its occurrence was dependent upon juvenile experience. Further, if a sensitive period during which the relevant experience must occur exists, it is apparent that its

termination is not before the twenty-fifth to twenty-sixth week of life. The apparent, slight homogamy observed in experimentals may be attributable to the more aggressive courtship of the Brown Leghorn cocks; crouching in hens may develop in the absence of heterosexual experience (Fisher and Hale, 1957), and also as a submissive response to dominant aggressive hens. Alternatively, it is possible that the slight homogamy tendency of experimentals in Series I tests reflects a truly innate response which was inhibited by the abnormal juvenile social environment (total heterosexual deprivation, but which could again be facilitated by a normal social environment (heterosexual experience). No degeneration of the innate mechanism would have occurred during deprivation. Analogous results have been reported for congenitally blind humans with restored sight (Senden, 1932) and for chimpanzees (Riesen, 1947).

Currently no firm conclusions as to the specificity of the relevant experience can be drawn. No observations were made on experimental hens during ontogeny, and thus the occurrence and possible affects of homosexuality cannot be assessed. Non-specific sexual experience (e.g. of heterogamic males) could conceivably facilitate the significant expression of the innate tendency to homogamy. If the first interpretation of the apparent slight homogamy tendency of experimentals were correct, it could be presumed that the relevant experience is highly specific, since it has already

been noted that Brown Leghorn hens respond to male plumage stimuli. If such is the case, then it is evident that relevant experience could not occur prior to 6-8 weeks after hatch, when sexual dimorphism develops. It could commence later than this stage of course, and the onset of sexual behaviour may be an important limiting factor in this respect. Further data are required to elucidate these speculations.

Brief reference should be made to some observations made on hens reared in the tri-breed flock alluded to previously. Both the testing conditions and numbers of hens involved render serious and statistical analysis of the results of alternate-presentation tests with males of the three breeds invalid. It should only be noted that some evidence of break-down of homogamy and of heterogamy as the result of mixed rearing was obtained. The heterogamy tendency was seen in White Leghorn females (c.f. corresponding results for males). Clearly homogamy is not irreversible or entirely stable in females or males.

Conclusions

Sexual imprinting may be important in orientating adult male sexual behaviour intra-specifically in wild precocial birds, but homogamy is a well developed trait in the domestic cock in the absence of any opportunity to so imprint to a parent. There is evidence to show that in wild, dimorphic duck species, males also respond innately to conspecific females (Schutz, 1965). Present results indicate, though by

no means conclusively, that a similar tendency may exist in the male chicken with respect to breeds (c.f. Guiton, 1962). It is not known whether sexual imprinting would be an important factor in effecting breed homogamy under more natural conditions. Whilst homogamy develops almost as strongly in socially-deprived males as in normal-experienced ones, it is apparent from the present study that it is a response to relatively unspecific stimuli. That this was so was evinced by three main findings. Firstly, non-white Crossbred females have equivalent stimulus valency to Brown Leghorn hens for Brown Leghorn cocks reared in normal or deprived juvenile environments; it was shown earlier in the study that White Leghorn males did not discriminate between hens of two all-white White Leghorn strains. Finally, Crossbreed males did not discriminate between white own-strain cues and white White Leghorn cues. It is possible that under natural conditions sexual imprinting could refine stimulus specificity (c.f. Guiton, 1962); in the present work, normally reared Brown Leghorn cocks exhibited a slightly stronger degree of homogamy than deprived ones in many cases, and thus learning which is not of the sexual imprinting type appears also to enhance sexual responsiveness in males.

Schutz observed that sexual imprinting to a heterospecific female resulted in the overriding of innate conspecific 'preferences' in male ducks. A similar phenomenon was seen in the domestic cock as a result of extensive experience of

heterogamic females during the juvenile phase. Moreover, limited heterosexual, heterogamic experience evoked some breakdown of homogamy in the adult phase also. If homogamy is an innate response, it is clearly not irreversible.

Imprinting to siblings (if it occurs in the present material) is probably an unimportant process in the orientation of adult sexual behaviour. Certainly it could not act in any direct manner and in the absence of subsequent reinforcing experience, since there is such an enormous disparity between chick and adult phenotypes. If this process is of any significance in homogamy in the Fowl, its affects are clearly reversible, and its importance must be limited, since males deprived of heterosexual experience from hatching exhibited homogamy. If, as suggested, experience does enhance sexual responsiveness, it is apparently experience occurring later in ontogeny than true imprinting processes, though its specificity must remain in question as yet.

The relative importance of innate and experiential factors in homogamy in females is not yet entirely clear. Females, like males, exhibit homogamy in the absence of opportunities to imprint in the classical sense. They <u>appear</u> to be more dependent upon experience than males, which is the converse of the picture presented for various dimorphic duck species by Schutz. For the normal expression of homogamy in the adult hen some previous experience is necessary, though its specificity remains unknown. It seems unlikely, however,

that sib imprinting or homosexual experience is adequate or important. One interpretation of present results leads to the suggestion of a sensitive period for the establishment of the homogamy response in hens, which would not be sharply delimited and restricted to a brief, early, ontogenetic phase. Its commencement, however, may be regulated by the time of development of sex dimorphism, but its upper limit would not occur prior to sexual maturity. Experience may enhance sexual responsiveness in females as well as males; hens may respond innately to male plumage colour releasers, but sexual experience may be necessary to enhance crouching (i.e. sexual receptivity). Homogamy is not an irreversible response in the hen, but it is not yet known whether sexual experience in the adult phase can exert the same affect on this trait as has been reported above for juvenile experience.

The affects of modifying the adult social environment on homogamy have only been examined so far in males. Only one of the experimental social environments studied affected homogamy significantly, and even in this case the affects were not universal amongst subjects kept in the experimental environment. Despite the lack of major behavioural differences between breeds of Fowl, homogamy had a considerable degree of stability in males. The heterogamic heterosexual environment abolished homogamy in the group of males subjected to it, whereas the homo-heterogamic heterosexual environment did not. Schutz reports similar findings in ducks with respect to early

social environment, but in the present study it was observed that rearing males in what were essentially "choice" conditions markedly reduced the level of homogamy and effected some degree of heterogamy. This finding indicates that social organisation in the mixed-breed flock may have exerted a strong affect on subsequent orientation of sexual behaviour. Schooland (1942) reared ducklings and chicks communally, and observed that in subsequent "choice" tests between con- and heterospecifics both selected conspecifics. His experiments were not concerned with sexual behaviour however. Purely visual interactions with other breeds failed to affect the level of homogamy significantly in present experiments. If analogies with wild syntopic species are at all valid in the present context, these findings suggest that such interaction would little affect homogamy in such species, but that the consummatory or reinforcing affect of interspecific mating would perpetuate this phenomenon if environmental conditions remained unchanged.

Finally, mention should be made of experiments currently being undertaken. A further analysis of the importance of juvenile experience in establishing homogamy in males is being made by rearing four males, each in total visual isolation from all other birds from hatch to sexual maturity, when simultaneous-presentation tests of homogamy will be administered to these males and to normally-reared controls. To test the specificity of relevant juvenile experience in

females, a flock of Brown Leghorn pullets is being reared from hatching with White Leghorn males only. Sexual isolation tests to be given in the adult phase should reveal further evidence as to the relative importance of innate and experiential factors in homogamy. To determine whether relevant and necessary experience must fall within a sensitive period, an attempt is being made to decide whether deprivation of normal experience at varying ontogenetic stages affects the subsequent orientation of adult sexual behaviour in the hen. It is hoped to determine ultimately whether any upper temporal limit exists in the adult phase, beyond which it is not possible to establish homogamy in sexually naive females.

CHAPTER V

The role of Aggressive behaviour in micro- and macro-evolutionary dynamics

Sewall Wright's (1932) model of theoretical population structure for optimal evolutionary progress, to which I referred in the introductory chapter, postulates a population split up into largely inbreeding, partially-isolated, sub-populations, between which there is a limited level of gene-flow. WRIGHT argues that this is the most effective mechanism for trial and error in the field of gene combinations. The importance of inter-population gene-flow is essentially twofold. Firstly, total isolation of populations leads to excessive inbreeding, a very small effective population size, and ultimately the deterioration and homogeneity typical of a closely inbred population. 'Exploration' of new niches or existence after a dramatic change in the existing niche becomes impossible due to the lack of genetic variability. Random fixation of non-adaptive gene combinations is likely. This can be counteracted by inter-population selection effected through migration, which increases the genetically effective population size.

Secondly, and the two points are not unrelated of course, there is a good chance in WRIGHT's model that a local population will reach a new adaptive peak (i.e. a particularly adaptive gene-combination arrangement), and it will then "pull the rest of the species with it up the

peak" if crossbreeding between populations exists. This mechanism makes for a far more rapid rate of evolutionary change than can pertain in a large, panmictic population.

Aggressive behaviour may have a role in effecting or strengthening reproductive isolation between social groups within a species or between related species. It is known that intruders entering a socially-organised group normally elicit aggression in group members (McBride, 1964). However, little is known concerning the parameters of inter-population gene-flow; behavioural and other agencies affecting migration and assimilation levels have hitherto not received much attention (Wood-Gush, 1963 and 1965). In this respect, it is pertinent to enquire into the many factors which may affect gene-flow, amongst which are the stimuli eliciting emigration, the social organisation of the host population, and the subsequent reproductive potential of assimilated immigrants. I propose to adopt the term 'effective immigrant assimilation rate' rather in the manner WRIGHT uses 'effective population size', to denote the actual rate of incorporation of immigrant genes into the host population gene-pool. Effective immigrant assimilation rate will thus be different from apparent immigrant assimilation rate in that it will refer only to those immigrants which are assimilated and able to contribute significant numbers of genes to the succeeding generations of the host population. In socially-organised populations,

aggressive behaviour oriented towards immigrants may affect the level of actual immigration, the social rank at which 'successful' immigrants are assimilated, and their subsequent reproductive contribution. It is this problem with which the present chapter is concerned.

Amongst the remarkably few analytical investigations of effective immigrant assimilation rate are several pertaining to the chicken and one pertaining to domestic dogs. The very nature of the problem demands both field and laboratory approaches. Guhl (1962) has summarised the relevant data for the Domestic chicken. Strangers introduced into an established flock elicit threat or overt attack in flock-members; they may retaliate, or more commonly they avoid flock members and congregate in some neutral area. If several strangers are introduced simultaneously as a group, they tend to congregate in a sub-group apart from the flock-members. Assimilation into the flock social structure may take some days or weeks, and is usually, though not invariably, at low levels in the social hierarchy. If immigrants are female and do not outnumber residents, they are thrown out of egg production for some time. Birds high in the social order have precedence at feed troughs, nests, roosts and dustbathing sites, and until the social organisation settles down once again, low-ranking immigrants may thus be at a disadvantage from the point of view of general health. Although low-ranking females

are generally copulated with more by males, their egg production is adversely affected; their genetic contribution to subsequent generations may thus be affected under pen systems of husbandry. Low ranking male immigrants are unlikely to contribute significantly either, since the dominance of top-ranking males precludes them from attaining many matings. It will be shown later (chapter VI) that much the same is true of Red Junglefowl in captivity, and Hale (1953) reported a similar phenomenon in the domestic Turkey. The phenomenon may be widespread in species possessing a hierarchical social organisation, and exert a considerable affect on effective immigrant assimilation rate. Finally, it is worth pointing out, that the production (egg) level of resident flock-members may also be adversdy affected by immigration (Guhl and Allee, 1944).

Apart from initial paired encounter and mixed-breed flock studies, there is little experimental data available on effective immigrant assimilation rate of breeds and strains into strange-breed flocks. Such studies are particularly pertinent in relation to the WRIGHT model and to the problem of gene-flow in populations generally. If the Wright model population structure is to be feasible, there must be gene-flow between populations already divergent to some extent. Discrimination against immigrants of differing phenotype could be an important factor affecting effective population size.

King (1954) studied the assimilation of individuals into socially-organised dog groups. He found that the breed of immigrants and the social-order rigidity of the established group were critical factors affecting assimilation. Aggression of group members was greatest towards immigrants of the same breed and sex, but the 'looser' social organisation of Cocker Spaniel groupings permitted of immigrant assimilation with far less disturbance than did the closed social grouping of Basenjis. These findings are in general agreement with the conclusions of Fisher (1964) for birds of various species, but not with those of McBride (1964) on chickens. This author found that in mixed flocks of four strains, which had been reared either communally or in single-strain flocks, there was greater agonistic interaction between than within strains.

Aggressive behaviour may also be of importance in the maintenance of established species as discrete entities, particularly related, syntopic species. Lorenz (1964) has said "If we put together into the same container, two sticklebacks, lizards, monkeys or boys, who have not any previous experience of each other, they will fight. If we do the same with two animals of different species, there will be peace - unless, of course, there is a predator-prey relationship between them". This is essentially true, provided we are not talking of related, syntopic species. Inter-specific aggression is common in most of the breeding

and maintenance activities of birds, particularly in those feeding, roosting, or nesting in mixed social groups (Fisher, 1964). FISHER categorises this aggressive behaviour into two types; hypersthenic, usually involving mistaken identity and "drive surplus" (extreme motivation), and taxogenic, usually having potential as an evolutionary mechanism. It is this latter category that concerns us here.

If inter-specific aggression functions as an ethological isolating mechanism, it must be restricted in its effective action to a relatively brief evolutionary time interval during the early phases of speciation. Reproductive isolation must not occur too early in the evolutionary process (Sibley, 1959), and when species have diverged to a considerable degree, they no longer possess the appropriate releasers of aggressive behaviour in other species. It is probably at the sibling species sort of level that aggressive behaviour has its greatest taxogenic potential.

Inter-specific aggression may function as an ethological isolating mechanism through the phenomenon of inter-specific territoriality. Lanyon (1959) has suggested that inter-specific territoriality may prevent the formation of mixed mating pairs, but Johnson (1963) and Orians and Willson (1964) disagree. The latter authors point out that inter-specific aggression may be expected when populations of two species come into contact for the first time. Indigo and Lazuli buntings, whose contact zone has been expanded by

recent human activity (Wells, 1958), and some species whose ranges are believed to have come into contact since the retreat of Pleistocene glaciation (Rand, 1949) are known to be inter-specifically aggressive, for example. The present author feels that we are not in a position to decide categorically whether interspecies aggression can commonly operate through the phenomenon of inter-specific territoriality as yet. It should perhaps be noted that there is no need to postulate a greater degree of aggression to prevent hybridisation between species than to permit of limited gene-flow between populations at an intra-specific level. At the species level, a whole complex of isolating mechanisms are usually in operation (Dobzhansky, 1949), of which aggressive behaviour would be but one.

There are, as has been intimated above, several known examples of interspecies aggressive behaviour, but few demonstrations of the role of such behaviour as an isolating mechanism. Lanyon (1957) has postulated that interspecies aggression is a secondary isolating mechanism between two closely related species of North American meadowlarks of the genus Sturnella, at what is probably an early stage in speciation. Dilger (1956) has imputed such a function to aggression between some catharid thrushes, and Hunsaker (1962) studied the isolating value of aggressive behaviour in the Sceloporus torquatus lizard species complex. The lastnamed author observed that male lizards attacked any

introduced lizard of similar size, but were not aggressive to con-specific or heterospecific males fifty per cent smaller than themselves that entered their territories. It is to be hoped that further examples will be forthcoming.

Kruijt (1964) has demonstrated that, in the Burmese Red Junglefowl, the motor elements of most of the sexual and agonistic behaviour patterns are fixed actions patterns, but that the way in which these patterns are released, oriented, and integrated is dependent to a considerable degree upon early social experience. In the wild, such experience is usually of conspecifics, and hence adult agonistic behaviour will usually be oriented towards con-specific individuals. In chapters I and IV it was shown that in the Fowl orientation of sexual behaviour in 'choice' situations may be largely innately determined in the cock, but much more experience-dependent in the hen. Males generalise in their sexual behaviour in such situations much more than females, not exhibiting own-breed bias in alternate-presentation situations. It is pertinent to ask whether such generalisation also typifies the orientation of male and female agonistic behaviour, since for aggressive behaviour to effectively function as an isolating mechanism, such generalisation would be imperative. If such generalisation exists, it would appear to indicate a fundamental difference in the mechanisms regulating the orientation of sexual and aggressive behaviour. On the other hand, if the orientation of aggressive behaviour

parallels that of sexual behaviour, and heterogamic individuals do not release aggressive responses, inter-breed aggressive behaviour would be limited and ineffectual as an isolating mechanism.

Two related, wild, syntopic species may possess the appropriate releasers of aggressive behaviour for each other. Where the orientation of aggressive behaviour is more experience-dependent, however, the isolating value of aggressive behaviour could become reduced. However, generalisation after con-specific experience has been observed in the Superb Blue Wren and related species (Rowley, 1965). When con-specific model males were introduced into the territory of male Blue Wrens, they were attacked, especially during the nesting season. A negative reaction to models of closely related sympatric species was observed, until experience with own-species models had occurred. Field observations revealed a lack of inter-specific aggression between the species under natural conditions.

From the foregoing remarks it will be clear that there are many points to be elucidated with regard to the role of aggressive behaviour in micro- and macro-evolution. This chapter is a description of two experiments (the first in a longer series which is being embarked upon) designed to test the efficacy of inter-breed and inter-strain aggressive behaviour as an ethological isolating mechanism in the Fowl. These experiments were carried out primarily to discover

whether birds of both sexes of normal experience exhibited aggressive behaviour towards heterogamic individuals, and whether agonistic behaviour showed the same own-breed bias in 'choice' situations as has been observed in the case of sexual behaviour. It was hoped that some light would be thrown on the similarity or dissimilarity of the mechanisms governing the orientation of agonistic behaviour in the adult Fowl.

Orientation of male agonistic behaviour in simultaneous and alternate-presentation situations

Material and Methods:

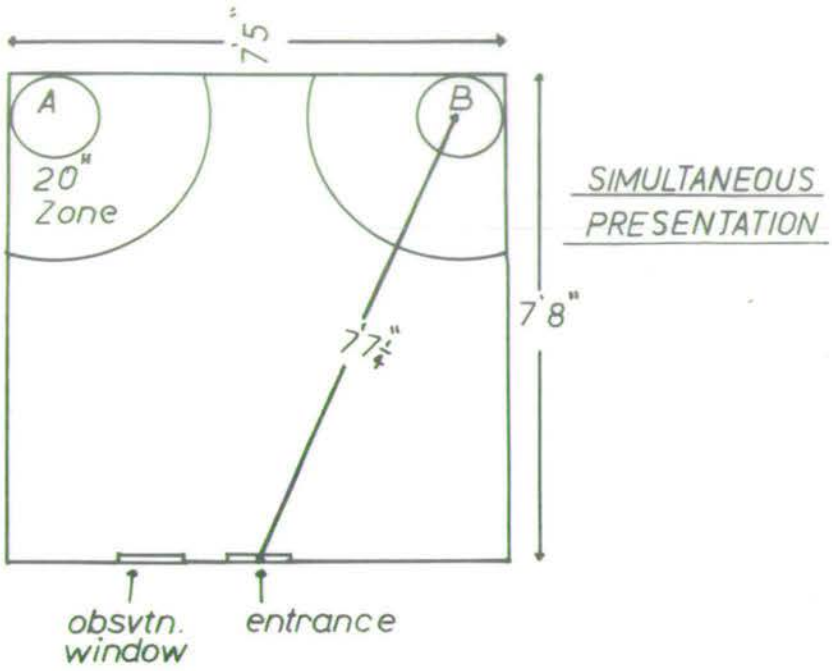
Twelve adult B strain (Brown Leghorn) males of normal (own-strain, heterosexual) juvenile experience were used in this experiment. They were released singly for six-minute periods into each of two test-situations (depicted in figure 14a). In the first, essentially a simultaneous-presentation situation, entry into the pen was via a tunnel equidistantly situated from two, cylindrical, wire-mesh cages, each containing a stuffed, model male, mounted in an upright posture. White lines delineated a 20" zone around the cages, the remaining pen area being considered neutral. The following measures of male agonistic behaviour directed to each of the cues (i.e. occurring within the cage areas) were taken:-

a. Orientation of initial aggressive responses.

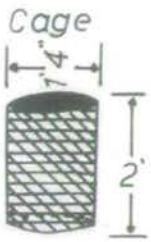
b. Total number of agonistic patterns (based on Wood-Gush, 1954 and 1956).

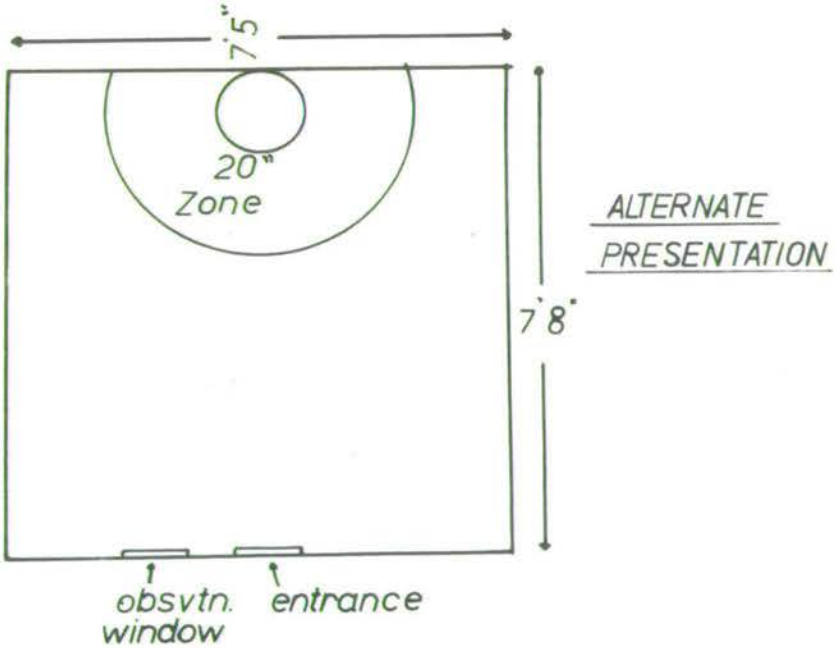
c. Occurrence of each individual agonistic pattern.

TEST PEN



SIMULTANEOUS
PRESENTATION





ALTERNATE
PRESENTATION

Figure 14a: Test situations used to study orientation of agonistic behaviour in adult cocks

In the second situation, essentially an alternate-presentation one, males were released into the same pen which now contained in any specific test only one of the two original male models; the cue was in one of the wire-mesh cages at the back of the pen and directly in line with the entrance tunnel. A 20" cage zone was demarcated round the cage. Each of the two original cues was presented during alternate six-minute tests. The following measures were taken:-

a. Entry into cage area.

b. Occurrence or lack of agonistic behaviour in cage area.

c. Occurrence of each individual agonistic pattern in the cage area.

In the simultaneous-presentation situation, the position of the cues was reversed in the second of the two tests each male had in this situation; each cock was tested twice with each cue in the alternate-presentation situation also, and the results were pooled. In the first experiment, tests in both situations were performed between 10.00 and 11.15, and 16.15 and 17.30, hours, and so arranged that each male received exactly the same treatment with regard to time of testing in both situations. Thus each male was tested once in the morning and once in the afternoon in each of the situations. In the second experiment, all tests were in the afternoon from 16.00 - 18.00, hours. In Experiment I, five day intervals were employed between simultaneous and alternate-presentation tests, and between the first and the replicate alternate-

presentation tests; satiation affects were thus precluded. However, such affects did not appear to be significant, and such inter-test intervals were not observed in Experiment 2. Experiment 1 lasted sixteen days, Experiment 2 only six days.

Model cues were used, since the response of live cues would have affected the agonistic behaviour of birds being tested and made analysis impossible. Use of models resulted in early waning of agonistic behaviour[1] of test males, and trial and error showed that a six-minute test duration was both suitable and meaningful. I did not deem it feasible to distinguish between the aggressive and fleeing tendencies occurring in agonistic behaviour, since such would be a rather arbitrary and subjective distinction. It is not felt that lack of such distinction in any way invalidates the conclusions to be drawn from this work. In testing females (reported later), this difficulty was less evident. In the present experimental situation threat displays and 'displacement activities' occur, but fighting and fleeing patterns do not. Waltzing is possibly the best gauge of threat behaviour.

---

[1] As defined by Scott and Fredericson (1951), but extended in meaning to refer also to the different motivational components of <u>individual</u> displays occurring in aggressive situations.

Results:

Experiment 1:-

Males were tested in both simultaneous and alternate-presentation situations with own-strain and S strain (White Leghorn) cue males.

Only one male failed to exhibit cue-oriented agonistic behaviour, and it failed to do so only in one simultaneous-presentation test. Significant biases in agonistic behaviour were observed in the simultaneous-presentation situation in one of the measures taken, and in the alternate-presentation situation in the same and an additional measure. Data for these two measures are summarised in a histogram (figure 15).

Simultaneous-presentation situation:-

Initial orientation of agonistic behaviour was not significantly cue biased ($p > 0.1$ in X^2 test); 69.6 per cent of initial orientations were to the Brown Leghorn cue, 30.4 to the White Leghorn cue. Only four cocks exhibited the same initial orientation in both tests, each showing own-breed bias on both occasions. No significant cue-bias was seen in either total agonistic behaviour patterns (t, 22 degrees freedom = 0.971, $p > 0.3$) or in individual patterns except waltzing. Males waltzed significantly more to own-strain than White Leghorn cues (t, 22 degrees freedom = 6.81, $p < .01$). No marked tendency to avoid the White Leghorn cue male occurred, and it elicited considerable agonistic behaviour.

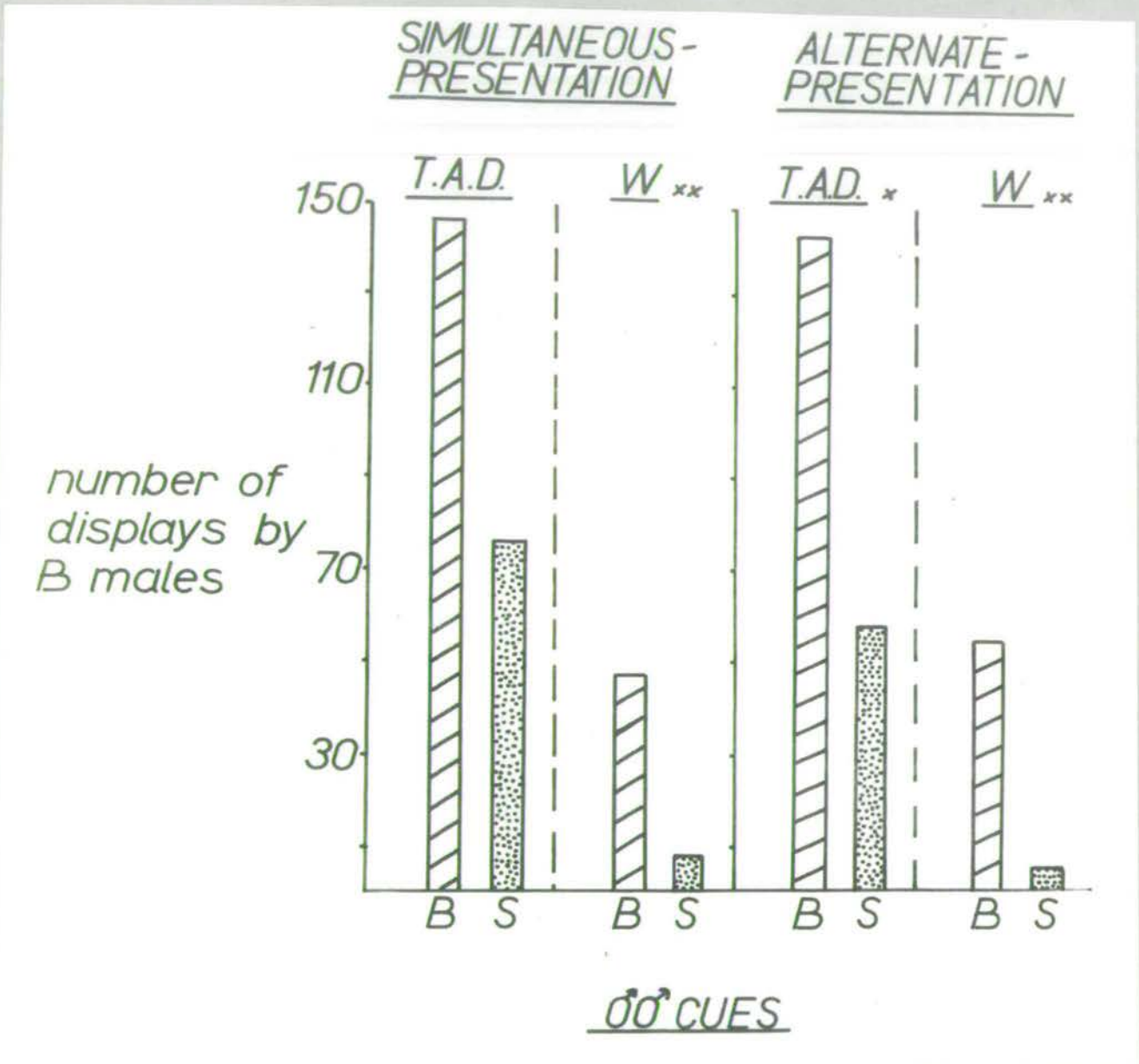

SIMULTANEOUS-
PRESENTATION
ALTERNATE-
PRESENTATION
T.A.D.
W xx
T.A.D. x
W xx
150
110
70
30
number of displays by B males
B S B S B S B S
♂♂ CUES

Figure 15: Orientation of agonistic responses of Brown Leghorn males during simultaneous and alternate presentations of own-breed and strange-breed male models

B = B line (Brown Leghorn)

S = S line (White Leghorn)

T.A.D. = Total Agonistic Displays

W = Total waltzes

X = significant difference at 5% level

XX = " " " 1% "

Alternate-presentation situation:-

No significant difference in entry of males into the cage area (i.e. approach to cue) was noted with the two differing cues. The Brown Leghorn cue elicited approach on nineteen occasions, the White Leghorn on sixteen. Agonistic behaviour was observed after all approaches except one. The Brown Leghorn cue elicited significantly more agonistic patterns and waltzes than the White Leghorn cue ($p < .05$ and $p < .01$ respectively). In no other agonistic behaviour category was cue-bias at a significant level seen.

Experiment 2:

The same twelve males were tested in both types of situation with B and W line (both Brown Leghorn) model males. In no test was cue-oriented agonistic behaviour entirely absent. The main findings are summarised in figure 16.

Simultaneous-presentation situation:-

The initial orientation of agonistic behaviour was not significantly non-random; in 70.83% of tests it was to the W cue, in the remainder, of course, to the B cue ($p > 0.1$). Nine males showed the same initial orientation in both tests, of which seven exhibited W-bias and the other two B-bias. The W cue elicited significantly more agonistic patterns ($p < .01$) and waltzes ($p < .01$) than the B cue male. No cue-bias was seen with respect to any other individual pattern.

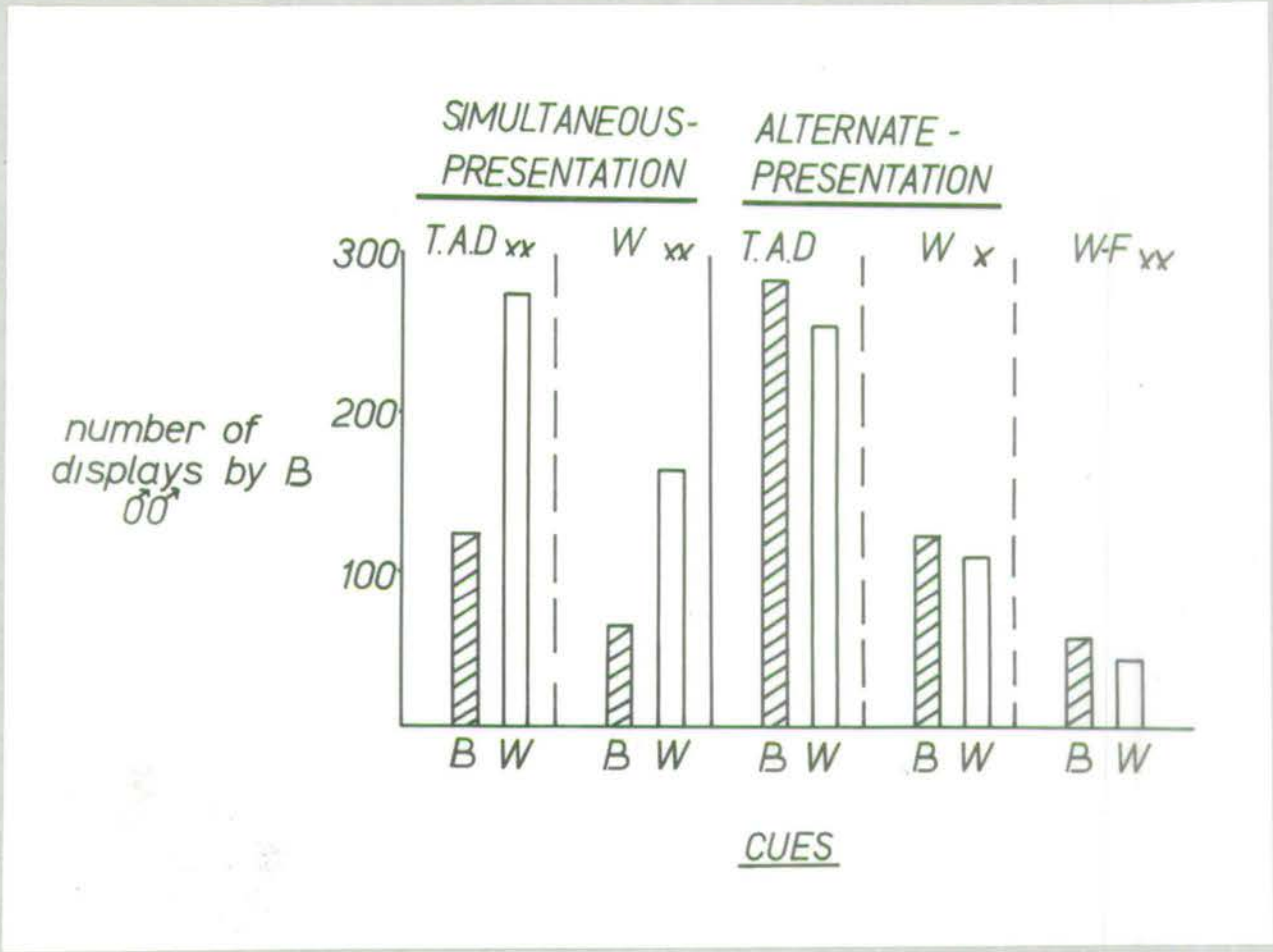

SIMULTANEOUS-
PRESENTATION
ALTERNATE -
PRESENTATION
T.A.D xx
W xx
T.A.D
W x
W-F xx
300
200
100
number of
displays by B
♂♂
B W
B W
B W
B W
B W
CUES

Figure 16: Orientation of agonistic responses of Brown Leghorn males during simultaneous and alternate presentations of own-strain and strange-strain male models

B = B line
W = W line
} Brown Leghorn

T.A.D. = Total Agonistic Displays

W-F = Total Wing Flaps

W = Total waltzes

X = significant difference at 5% level

XX = " " " 1% level

Alternate-presentation situation:-

Approach was elicited by the cues in 47 of 48 cases, and agonistic behaviour was seen in all forty-seven instances. No overall bias in the orientation of agonistic behaviour was seen ($p < .5$), but the B cue elicited significantly more waltzing than the W cue ($p < .05$). The B cue also elicited significantly more wing-flapping than the W cue ($p < .01$), and this display is thought to be one with a strong, aggressive component. No cue-bias was observed in any other facet of agonistic behaviour.

In the inter-breed experiments, the twelve Brown Leghorn cocks showed a significantly greater amount of agonistic response to the own-breed cue male. Thus males of similar juvenile experience exhibit similar biases in both agonistic and courtship behaviour at the breed level when tested in simultaneous-presentation conditions; but whereas non-randomness of courtship was extremely rare under alternate-presentation conditions, this was not the case with agonistic behaviour at either inter-breed or inter-strain levels. The conflicting results obtained in alternate and simultaneous-presentation tests involving B and W line cues remain puzzling, although I have no strictly comparable results for courtship behaviour with which to compare them. It is interesting to note that discrimination is particularly marked in waltzing; this is the one agonistic pattern occurring in the present experimental conditions that is clearly oriented towards the other combatant

during agonistic encounters between living birds. This display is known to have a strong aggressive element and can be regarded as true threat behaviour. It is realistic to regard cue-bias in waltzing as a genuine cue-bias in aggressive (as opposed to agonistic) behaviour.

Males of normal juvenile experience clearly generalise in their subsequent adult agonistic behaviour to other breeds and strains to a considerable degree.

Affects of temporary immigration from other breeds on agonistic behaviour in established flocks of hens

Material and Methods:

Two female flocks, of six and seven Brown Leghorn hens respectively, were studied. Each flock had been established some months prior to experimentation, and all flock-members were of normal juvenile experience. The flocks were kept in visual isolation pens, 8' x 6' in area. The social hierarchy of each flock was established prior to experimentation by a scanning technique and observing encounters after food deprivation.

Eight B (Brown Leghorn) and eight S (White Leghorn) line female immigrants of comparable age to the flock members were introduced into flock Y for one half-hour test. Introductions were made every third day at 13.00. and 17.15. hours. On any one test day, one B and one S immigrant female were introduced, and the order of introduction was reversed on alternate test days. Immigrants were generally taken from other

established flocks of appropriate breed. The same procedure was adopted with flock X, except that introductions were at 12.30. and 16.15. hours, and immigrants were B line and Alpha Crossbred females. The Crossbred and most of the Brown Leghorn immigrants were caged individually during the experiment. All birds, as implied earlier, were individually labelled to facilitate rapid recognition by the observer, and the following behavioural measures were taken for both flock-members and immigrants:-

a. Identity of bird attacking or threatening spontaneously first.

b. Latency to attack or threaten spontaneously first.

c. Spontaneous threats and attacks.

d. Retaliatory threats and attacks (especially the percentage of spontaneous attacks and threats evoking retaliation).

e. Fleeing and avoidance responses.

f. Submissive postures.

g. Outcome of overt fights.

h. Identity of individual flock-members exhibiting attack, threat and overt fighting behaviour.

The introduction of B line immigrants not only acted as a control, but facilitated a strict comparison between agonistic responses of flock-members to familiar and unfamiliar phenotypes. It also enabled the author to study effective immigrant assimilation rate of birds of like phenotype to the host population.

Results:

Table 11 is a summary of the data acquired from both flocks.

Flock Y:-

Flock-members were the first to behave aggressively (i.e. spontaneously threaten or attack) far more in tests with own-breed immigrants than in tests involving S line immigrants. Latency to react aggressively to immigrants was significantly lower for tests with B immigrants than for tests involving White Leghorn immigrants (mean 72.3 secs. as opposed to 820.0 secs.). Although some habituation of low-ranking flock-members to S female immigrants did occur towards the end of the experiment, the general reaction was one of extreme alarm and marked avoidance. B immigrants were spontaneously threatened significantly more than S immigrants ($p < .02$), and spontaneous attack yielded similar results, though lack of spontaneous attack on S females precluded statistical analysis. When one considers level of spontaneous attacks and threats together as the level of spontaneous aggression, it is clear from results that B immigrants elicited significantly more aggression in flock-members than did S immigrants ($p < .01$). This was not attributable to the greater aggressiveness of the B immigrants, since a) the most aggressive B immigrants were attacked least and b) the least aggressive ones were attacked significantly more than comparably passive S immigrants. The greater level of spontaneous

Table 11

Reciprocal agonistic behaviour between resident-members of two female Brown Leghorn flocks and immigrants of the same and other breeds (Experiment I above, Experiment II below)

Immigrant strain & host flock	Attacked or threatened first	Mean latency (secs.) to attack or threaten first	No. of spontaneous threats	No. of retaliatory threats	No. of spontaneous attacks	No. of retaliatory attacks	Fleeing & sub-missive responses	%age of fights won
Immigrant S	3	1012.3	5	1	1	2	79	100
Host Flock Y	3	820.0	25	3	0	2	92	0
Immigrant B	2	38.5	44	23	23	29	261	48.8
Host Flock Y	6	72.3	152	7	78	27	156	42.2
Immigrant CBR	0	-	0	1	0	2	932	0
Host Flock X	8	15.6	129	0	374	0	3	100
Immigrant B	0	-	17	9	11	25	386	37.5
Host Flock X	8	65.0	179	3	114	17	75	54.2

Legend in text.

aggression elicited by B immigrants was thus a reflection of the greater stimulus valency of factors other than aggressive behaviour. Flock Y members did not exhibit differences at a significant level in their flight and submissive behaviour to the two immigrant phenotypes; within-strain variation was high however, due to differences in the degree to which individual S immigrants and flock-members came into proximity, and to the outcome of early encounters in B immigrant tests. The percentage of total fights won by immigrants and the degree of fleeing and submissive behaviour of flock-members were broadly correlated. 37.3% of spontaneous aggressive patterns exhibited by Brown Leghorn immigrants elicited flock retaliation, 42.86% of those shown by S (White Leghorn) immigrants elicited retaliation; the difference was not significant. Only one fight occurred in S immigrations, but flock-members won 42.2% of the forty-five fights occurring in Brown Leghorn immigrations.

A comparative analysis of the agonistic behaviour of the Brown and White Leghorn immigrants, revealed some interesting differences. Mean latency to attack was significantly higher for White Leghorn immigrants due to mutual avoidance by immigrants and flock-members in S introduction tests. Significantly more spontaneous attacks emanated from B than S temporary immigrants ($p < .05$), and B immigrants exhibited significantly more spontaneous aggressive patterns than S females ($p < .05$). No significant difference in fleeing and

submissive behaviour was observed, the percentage of fights won by B immigrants being broadly correlated in a negative manner with the occurrence of fleeing and submission in these birds. No significant difference between immigrant breeds in the level of retaliatory aggression was seen.

Table 12 indicates the relationship between dominance status of flock-members and their aggression towards B and S immigrants. No significant correlations of this type were observed, except that a slight degree of habituation to White Leghorn immigrants that occurred towards the end of the experiment was manifested only in the three lowest-ranking flock-members. Distribution of immigrant-oriented aggression among flock-members was not significantly correlated in the two types of immigration.

Flock X:-

Alpha Crossbred immigrants elicited more spontaneous attacks ($p < .01$) and total spontaneous aggressive behaviour patterns ($p < .05$) than B immigrants. All Crossbred immigrants were extremely submissive throughout tests, and were attacked relentlessly. Lack of retaliation by these immigrants did not entirely account for their greater stimulus valency however, since no marked correlation between degree of retaliation by B immigrants and degree of spontaneous aggression of flock-members to them was noted. Other stimulus properties of Crossbred immigrants were clearly involved. No significant difference in fleeing and submissive behaviour of flock-members

Table 12

The effect of social rank on female aggressive behaviour towards immigrants of own- and other breeds in Flock Y

Flock A member	Spontaneous threats	Spontaneous attacks	Retaliatory threats	Retaliatory attacks	Fight Outcomes	
Hen 36	15	7	2	6	won	2
					lost	4
Hen 93	30	15	3	5	won	3
					lost	2
Hen 92	43	22	1	7	won	5
					lost	5
Hen 13	12	4	0	1	won	1
					lost	0
Hen 11	16	6	1	3	won	0
					lost	4
Hen 65	36	19	0	5	won	3
					lost	4
Responses to Brown Leghorn Immigrants						
Hen 36	0	0	1	0	won	-
					lost	-
Hen 93	0	0	0	0	won	-
					lost	-
Hen 92	0	0	1	1	won	-
					lost	-
Hen 13	2	0	0	0	won	-
					lost	-
Hen 11	19	0	1	1	won	0
					lost	1
Hen 65	4	0	0	0	won	-
					lost	-
Responses to White Leghorn Immigrants						

Female flock-members are given in order of social rank (top to bottom) indicates lack of dominance relationships between a pair. Red lines indicate mutual tolerance behaviour, thickness of line is indicative of degree of tolerance.

with the two immigrant breeds was seen; the high overall level of this type of behaviour during B introductions was the result of high levels in only a few such tests in which excessive fleeing occurred. Differences in the outcome of fights are of doubtful significance due to disparity of fight incidence in the two types of immigration.

In no test did an immigrant behave aggressively before flock-members exhibited aggression towards it. Significant differences in the responses of the two immigrant breeds to flock-members were observed only with respect to fleeing and submission, retaliatory aggression, and the outcome of overt fighting. Crossbreed immigrant hens fled or adopted submissive postures significantly more than B line immigrants ($p < .01$), retaliated to a significantly lower percentage of spontaneous aggressive activities of flock-members ($p < .02$) and won a significantly smaller percentage of fights.

In table 13 the effect of flock social structure on aggressive behaviour of flock-members to the two immigrant breeds is summarised. No overall correlation between social rank and level of aggression to all immigrants was seen. The distribution of aggressive behaviour orientated to immigrants among flock-members was not the same with respect to the two different immigrant phenotypes.

The results obtained for flock Y paralled those obtained in Brown Leghorn females of similar experience for sexual behaviour. In both sexual and agonistic contexts, own-breed

Table 13

The effect of social rank on female aggressive behaviour towards immigrants of own- and another breed in Flock X

	Hen 8	Hen 20	Hen 41	Hen 24	Hen 87	Hen 90	Hen 33	
Spontaneous threats	12	20	25	21	44	33	12	Responses to Brown Leghorn Immigrants
Spontaneous attacks	18	2	13	3	41	10	21	
Retaliatory threats	0	0	0	0	1	0	1	
Retaliatory attacks	0	1	1	2	5	1	4	
Fight Outcomes	won 1 lost 1	won 0 lost 0	won 0 lost 0	won 0 lost 1	won 3 lost 1	won 0 lost 1	won 0 lost 1	
Spontaneous threats	19	20	28	3	12	40	15	Responses to White Leghorn Immigrants
Spontaneous attacks	54	59	84	5	18	49	48	
Retaliatory threats	1	0	0	0	0	0	0	
Retaliatory attacks	1	1	1	0	0	0	0	
Fight Outcomes	won 2 lost 1	won 1 lost 0	won 1 lost 0	won 0 lost 1	won 0 lost 0	won 1 lost 0	won 0 lost 0	

Flock-members given in order of social rank (left to right). A triangular dominance relationship existed in this flock. Red lines indicate mutual tolerance behaviour between flock-members.

individuals possessed greater stimulus valency than White Leghorns for Brown Leghorn hens. However, the same cannot be said in respect of Crossbred females, which elicited stronger aggressive tendencies in Brown Leghorn hens than own-breed females, the exact opposite of findings reported earlier for sexual behaviour.

The data for flock X are, however, reminiscent of observations made during alternate-presentation sexual isolation tests of normal-reared Brown Leghorn hens (see Chapter II), in which Crossbred males elicited more aggression in the females than Brown Leghorn males. In those tests, White Leghorn cocks also elicited considerable aggression in Brown Leghorn females, and less marked fleeing and avoidance than that reported above for the present experiment. In an experiment described on page 88 (Chapter IV), alternate-presentation tests of sexual isolation were given to a flock of normal-reared Brown Leghorn hens, to which Crossbred, White Leghorn and own-breed males were presented singly. Particular attention was paid to threat behaviour of females and to agonistic encounters between the sexes. Findings were similar to the present ones, Crossbred males having a greater stimulus valency (for aggressive behaviour) than Brown Leghorn males, which in turn stimulated more female aggression than White Leghorn males.

In both Y and X flocks, results indicated that discrimination by flock-members, and immigrants was not entirely

dependent upon agonistic behaviour. There were, naturally, some reciprocal affects of agonistic behaviour between immigrants and flock-members. Moreover, there was some evidence that agonistic behaviour between immigrants and particular flock-members exerted an affect on agonistic responses of non-participant flock-members, towards immigrants. Finally, the outcome of immigrant-flock-member encounters early on in tests generally determined the pattern of subsequent agonistic behaviour during the test.

Conclusions

In the SEWALL WRIGHT population model, a limited degree of gene-flow between populations undergoing some genetic divergence is postulated through the agency of migration. In the introduction to this chapter, I pointed out that we do not at present know whether such gene-flow could occur in natural populations, and that there is a small body of evidence to suggest that certain hitherto largely ignored factors may limit gene-flow and gene-recruitment in such populations. The concept of effective immigrant assimilation rate was advanced as one worthy of analysis. The present results obtained from a domestic species enable us to examine the affects of aggressive behaviour and social organisation of the potentially recipiant host population on effective rate. Moreover, it is possible to examine the behaviour of the immigrants themselves in order to determine whether this may also impose some restriction on assimilation.

Experiments with both males and females have been concerned with reactions to individuals of like and unlike phenotypes; experiments with females, in particular, facilitate the analysis of potential assimilation rate of genetically divergent and genetically similar populations.

The results of experiments with males indicate a considerable tendency to generalise in agonistic behaviour i.e. males of similar and differing phenotypes both elicite aggression in males of normal early experience. Males did not exhibit marked avoidance tendencies towards males of other breeds or strains, though it should be emphasised in this context that model cues were used. In absolute terms, an own-breed bias in agonistic behaviour was observed in 'choice' situations, but an own-strain bias was seen only in alternate-presentation conditions. It is concluded that males of slightly or very different morphological characteristics elicit aggressive behaviour in males of own-strain early experience to a degree likely to exert some restricting influence on male immigration between 'populations' differing to such extents. Territorial effects, which might reasonably be expected to strengthen such gene-flow barriers, were absent from the experimental situation used for males.

Experiments with 'territorial' groups of females indicated a tendency to generalise which was perhaps rather less marked. Own-breed bias in aggressive behaviour was seen only in tests involving own-breed and White Leghorn immigrants; initial

reactions to White Leghorn immigrants were of alarm and avoidance, not aggression. However, in the final stages of this experiment some habituation and aggression to White immigrants was seen. In tests involving Crossbred temporary immigrants it was noted that such immigrants elicited a greater level of aggression in Brown Leghorn-flock-members than did own-breed immigrants, and the level was such that, on a short-term basis at least, effective immigrant assimilation rate would have been drastically affected. The affect of territoriality *per se* has not been analysed in the present work; it is felt that its presence in the test-situation enhances the analogy between this situation and that pertaining in the micro-evolution of wild animals. Present results also show that behaviour of immigrants themselves may not necessarily always enhance their assimilation into populations, though adoption of submissive postures may facilitate assimilation to some extent.

It was found that social rank of flock members did not exert much affect on their aggressive responses to immigrants. However, if both resident Brown Leghorn flocks are considered, it becomes apparent that there was a spectrum of "successful" immigration of Brown Leghorn temporary immigrants, ranging from total domination of certain immigrants by all flock-members to the converse situation. The inference was that effective assimilation of immigrants of the same phenotype was by no means negligible, though of course other factors

which could affect subsequent reproductive success of assimilated immigrants were not studied. Present findings differ from those cited by Guhl (1962) in that when "successful" immigration took place it was not invariably at low levels in the flock hierarchy. Since it is not certain that the 'rank' attained by Brown Leghorn immigrants in the present experiments was more than temporary, the disparity between the results in question and the ones here reported may be an experimental artifact.

It would be of considerable interest to make comparative studies of effective immigrant assimilation into species of differing social organisation. Jenkins (1961), for example, has found that in the partridge (Perdix perdix), in which there is no social hierarchy within coveys, little intra-familial mating occurs, and pairing often takes place between individuals of different coveys. Indeed in many species with coveys, there appears to be a good deal of migration between coveys (Errington and Hamerstrom, 1936; Sumner, 1935; Gullion, 1962 and pers. comm.). On the other hand, the Bruce effect (Bruce, 1959; Bruce and Parkes, 1960) would seem to mitigate against a high level of effective immigrant assimilation in mice.

Interspecific aggression may function in maintenance of species as discrete entities. It is interesting in this connection to find that such behaviour has isolating potential for breeds and strains of chicken differing chiefly in plumage

colour, body conformation and size. Experiments with males entailed the use of model cues; since aggressive behaviour was elicited in Brown Leghorn males by models of different colour, it is apparent that other morphological characters possess stimulus valency for aggressive behaviour.

At this early stage in the study, it is not possible to determine finally whether the orientation mechanisms for aggressive and sexual behaviour of adult Fowls are essentially similar or not. Certainly in adult females, the orientation of aggressive behaviour towards other breeds is not strongly dependent on the sex of the other-breed individual. Superficially, the orientation of both types of behaviour seems to be similar, with the high level of aggression exhibited by Brown Leghorn hens to Crossbred female immigrants being the only exception. One such bias was also observed with respect to sexual behaviour in Crossbred females (page 32). Further experiments are in progress.

Present findings resemble those of King (1954) for dogs, but although peck-order in flock X was less rigid than that in flock Y, no positive correlation between rigidity and 'acceptance' of immigration was discernible. Since different immigrant breeds were concerned in each case, a strict analogy with KING's work is precluded. Although my results are somewhat at variance with McBride's (1964), his strains were more similar than the ones used in this study; also, I have illustrated above how Brown Leghorn cocks of normal experience

reacted more strongly to W line than own-strain male models in simultaneous-presentation situations.

Experiments to determine the affects of early social environment on adult orientation of aggressive behaviour are under way. It is also hoped to study in more detail those factors which might affect the reproductive potential of assimilated immigrants by more long-term immigration experiments. Immigration into heterosexual groups may also have considerable relevance to micro-evolutionary problems, but more detailed study of the stimuli affecting emigration must remain largely the province of the field worker.

CHAPTER VI

Non-random mating in captive Red Junglefowl and at an intra-strain level in the Domestic Fowl

Part I

A general discussion of the intra-specific non-random mating phenomenon in wild and captive animal species

The elucidation of the genetical, evolutionary, and ecological significance of intra-specific non-random mating systems still awaits serious inter-disciplinary investigation at the experimental and observational levels. Comparatively little is known or understood of the distribution, underlying mechanisms and functional significance of this phenomenon. This section outlines existing theoretical considerations and actual observations of intra-specific non-random mating. It has been written not only to introduce the account of assortative mating in two subspecies of *Gallus gallus* which follows, but also to point out the fundamental problems which should concern workers in this field.

Darwin (1871) developed a theory of sexual selection to explain the evolution of secondary sexual characters in animals, whose evolution could not be adequately explained by the theory of Natural Selection. What is particularly pertinent in the present connection is that he visualised such a process operating through a non-random mating system involving inter-male combat and marked female "mate-choice". More recent writers have pointed out that the invocation of sexual selection to account for the development of secondary sexual

characters in many species is unnecessary and erroneous (Huxley, 1938; Moody, 1961). A lengthy discussion of the evolution of sexual selection would be out of place here; most modern evolutionary students probably agree that the phenomenon does in fact occur, but with a more restricted distribution than Darwin suggested. It is undoubtedly most strongly developed in polygamous and promiscuous species, particularly in those with communal arena or harem mating systems, and the reasons for this have been given by Huxley (loc. cit.) and Selander (1965) amongst others.

That sexual selection occurs in such species through the agencies of non-random mating systems is almost a truism. Nevertheless, it would be nice to have some actual demonstrations that this is so. Moreover, such systems afford ideal examples for determining in detail how non-random mating operates in effecting sexual selection; the relative affects of inter-male interactions and female "mate-choice" in determining the copulation incidence should be examined. The degree of refinement of sexual selection imposed by non-random mating within supposedly intrinsically non-random mating systems (particularly 'lek' systems) also merits attention. Finally, the overall affects of sexual selection operating through a non-random mating system on the evolution of particular species are of great importance. The affects which should be examined in this connection are those on mortality rate, general adaptiveness and rate of evolutionary

change, though such affects would indeed be difficult to study.

Wynne-Edwards (1962) has attributed to polygamy and non-random mating, particularly, but not exclusively, in harem and communally-displaying species, the function of regulating population density and dispersion. To state his arguments simply, polygamy and non-random mating place the effective control of mating in the hands of a few individuals; these individuals are in some way 'conditioned' by the amount of mating which has been undertaken personally or communally, and are able to with-hold coition once the appropriate quota of females has been fertilised. Thus non-random mating is regarded as a refinement of the homeostatic apparatus of the population which restricts reproductive output to a level compatible with group survival under the prevailing conditions of food supply. Social aggregations are viewed functionally as means of "assessment" (my word) of population density. Wynne-Edwards theory is essentially one of group as opposed to individual selection, and whilst agreeing that group selection may occur, the present author feels that Wynne-Edward's theories a propos of non-random mating lack both logic and serious supporting evidence. Some evidence has recently appeared (Kruijt and Hogan, 1964; Selander, 1965) to indicate that his arguments do not hold good with regard to two polygamous and promiscuous species at least. Kruijt and Hogan, for example, demonstrated by presenting model

grey-hens and timing natural matings, that the type of disinclination to mate and constraint on copulation postulated by Wynne-Edwards for the Black-cock did not exist on the two leks they studied. However, the potential of non-random mating as a factor regulating population density is worth some serious analysis, and perhaps 'lek'-displaying species afford the best possibilities for such studies.

In the introduction to this paper, I stressed the potential significance of the mating system in affecting effective population size, and also the importance of the latter concept in micro-evolution. Non-random mating effectively lowers the effective population size, and as Wright (1932) has suggested, effective population size (intimately bound up with population structure) exerts a strong affect on the rate of evolutionary change within the population. Non-random mating is potentially a mechanism increasing the inbreeding coefficient of populations, and as Sewall Wright pointed out, too great a degree of inbreeding in an isolated population leads down the slippery slope to extinction. On the other hand, a certain degree of inbreeding in partially-isolated sub-populations is theoretically necessary if the optimal evolutionary rate for the population as a whole is to be attained.

Gilliard (1963) has suggested that species of bird exhibiting arena display are evolving at an accelerated rate, more rapidly than other avian species. He further claimed

that the biological advantage of arena behaviour may be precisely that it does speed up evolution, but did not point out what advantage this had for the species concerned. The accelerated rate of evolution in such species is of interest, however, for an additional factor to those mentioned by Gilliard in causing acceleration may be that the population structure, especially in true lek species, is one facilitating the optimal evolutionary rate of change (i.e. resembling the Sewall Wright model). It must suffice for the moment to point out that the importance of non-random mating as a micro-evolutionary agent has not received the attention it deserves (see Wood-Gush, 1963).

Having outlined the importance of the phenomenon, it now remains to refer briefly to the information which has been gleaned as to the occurrence and nature of intra-specific non-random mating. A survey of literature revealed many anecdotal accounts, but for present purposes it is intended to confine discussion to well authenticated examples in the main. Examples from domestic and captive species have been included, since they often reveal a type of non-random mating which is also known in wild, related species, and hence furnish us with additional information.

Non-random mating systems are particularly well developed in many polygamous, promiscuous, and highly social species. Dominance relationships amongst males are important in effecting non-random mating in many hierarchically-organised

and harem species, though female mate-selection may be exercised in the initial stages of harem formation. Characteristically in such species, dominant males preclude the mating of subordinates by overt aggression or threat. This is so in captive lions (Allee, 1950), whilst in many polygamous seals and sea-lions, 'master' bulls secure large harems and stop other males from mating with their harem females (see Wynne-Edwards, 1962). It seems likely that similar phenomena occur in some whales (Beale, 1839) and rabbits (Thompson and Worden, 1956), and possibly in some deer species. Banks (unpublished) observed the rarer phenomenon of female interference in mating in the domestic sheep.

Non-random mating effected largely by so-called female "choice" (differential responsiveness of females) has been recorded in crabs of the genus Uca (Crane, 1941) and some spiders (Peckham and Peckham, 1889 and 1890). Geis and Elbert (1956) noted a correlation between cock tail-length and harem size in Ring-neck pheasants, and both captive hen Chukar partridge (Stokes, 1961) and female Ruddy Sheld-duck (Heinroth, 1911) are reported as responding sexually more to certain conspecific males than others. Similar differential responsiveness of females has been noted in a few other species and may be widespread. It is not confined in birds to polygamous and promiscuous species; McKinney (unpublished) described male display aggregations in

Green-Winged Teal, in which females 'selected' one particular male with which to pair. In this case, however, the chosen male's "success" in hostile encounters with other males in the display group was essential for the establishment of a firm pair-bond.

In arena-displaying species, differential female responsiveness, inter-male social relationships, and male strategy may all be important in varying degrees in effecting non-random mating in various species. Amongst gallinaceous species exhibiting such behaviour, the Greater Prairie Chicken (Tympanuchus cupido americanus), Sage Grouse (Centrocerous urophasianus), and Sharp-tailed Grouse (Pediocetes phasianellus campestris) described by Scott (1950) are characterised by lek systems in which mating is restricted to one or a few dominant males out of often very large numbers of males on the lek. In the Prairie Chicken, the master cock maintains his status by fighting, but may be attacked during mating; in the Sage Grouse, Scott saw a dominant cock perform 74% of the matings, actively preclude subordinates mating, but remain unmolested during his own mating activity. Male interference in mating also occurs in Sharp-tails.

In the European Black Grouse (Lyrurus t. tetrix), Kruijt and Hogan (1964) described a lek on which 85% of the matings in two seasons were performed by four central cocks. In analysing the underlying mechanisms, these authors concluded that female choice was important, and that dominance relation-

ships between males did not have a strong direct affect. Lumsden's (1961) account of a Capercaillie 'lek' suggested that non-random mating was occurring, but no male interference was observed. In wild turkeys (Meleagris gallopavo intermedia), Evans (1961) noted that a few males were dominant at the display-ground and chased others away. Thereafter, only the dominant stags displayed.

Amongst other arena-displaying species, non-random mating has also been observed. Hogan-Warburg (1964) has described the immensely complicated lek of the Ruff (Philomacus pugnax), and the fact that mating is not randomly distributed amongst the various categories of male. In Jackson's Whydah certain cocks are more attractive to hens than others (Van Someren, 1958). As in many other lek species, the females of the Black and White Manakin (Manacus manacus) visit the lek more than once and will display with more than one territorial male (Snow, 1962). Certain males are more attractive to the females than others; in the case studied in detail, the males holding central territories were most attractive (Snow, pers. comm.). In some lek-displaying species, females 'choose' particular territories rather than particular males. In the Uganda Kob (Buechner, pers. comm.), where there is marked non-random mating, territory maintenance by individual males is much less protracted than in the bird species alluded to above, and there is a high rate of interchange of males on the few "preferred" territories. Thus it may well be that

the genetical and ecological consequences of non-random mating in this species are rather different from those in other lek species.

In summary, it is apparent that several factors can be important in effecting non-random mating. Which factor is of paramount importance depends upon the social structure and organisation of the particular species involved. Two main types of mating system facilitate non-random mating in rather different manners. In lek species particularly, non-random mating is the result of several interacting factors, and may be a complicated process. The serious evaluation of the non-random mating phenomenon still awaits the amassing of a great deal of detailed and comparative data for all or most of the species exhibiting this type of behaviour.

Part II

A description and analysis of non-random mating in captive Junglefowl and in a strain of Brown Leghorn chickens

The main purpose of this study was to discover something of the type of mechanisms effecting non-random mating in two hierarchically-organised sub-species of phasianid. It is in the elucidation of mechanisms that laboratory model studies can contribute to our knowledge, since they permit of greater manipulation of variables including environment. Clearly care should be exercised in the application of theories derived from the results of such studies to situations in the wild. The usefulness of the present results is enhanced by the fact that several wild species exhibit social hierarchies, and by some resemblance of present testing conditions to lek and harem systems.

It was hoped also that comparison of the social and sexual behaviour of the two sub-species would shed a little additional light on their affinities, and perhaps in consequence on the enigmatical problem of the ancestry of the Domestic Fowl (see Hutt, 1949). Further, the type of mating system existing in wild junglefowl is virtually unknown, though Beebe (1918 to 1922) has alluded to the possibility of lek and/or harem display in the wild. Thus the type of experimental mating systems examined in this section may indicate a little of the propensities in mating behaviour of wild conspecifics. Evidently only very limited and tentative conclusions as to the latter can be drawn from the present

study. So little is yet known of non-random mating, that any approach seems both justified and welcome at this stage of investigation.

References in the literature to non-random mating in chickens are too numerous to mention in their entirety. Most of the early accounts were anecdotal and unanalytical, or fictitious (Chaucer c.1478; Hewitt, in Darwin, 1871; Wilkins, 1915; Heuser, 1916; Philips, 1919). Whilst such accounts are of interest, it does not really further our state of knowledge much to learn that, for example, "the female almost invariably prefers the most vigorous, defiant and mettlesome male!" In 1928 Upp observed non-random mating, but his claim that males exhibited 'preference' cannot be upheld, since he failed to take into account differential female receptivity. Similarly, the claim to have demonstrated non-random mating by Warren and Kilpatrick (1929) is not acceptable, since they did not actually observe the birds, but judged non-random mating to have occurred from the results of incubation tests. Murchison (1935 a and b) found that one hen in a flock was trodden more than its flock-companions, but said that male 'preference' was not involved. Skard (1937) observed non-random mating and some correlation between female peck-order and the "degree of appeal" of hens to the cock.

American studies of Guhl (1942 and 1951), Guhl, Collias and Allee (1945), and Guhl and Warren (1946) have revealed

that hens may "prefer" one rooster in a heterosexual flock containing several, though they do not react to social status as such. In heterosexual flocks, male social rank, sexual activity and interference in matings are broadly, if not absolutely, correlated; top-ranking cocks often sire most offspring, and female social rank, rate of mating and rate of soliciting the male are negatively correlated. Top-ranking hens are usually courted more than low-ranking ones however. Guhl also demonstrated that subordinate males may elicite more female solicitation than the alpha male. Wood-Gush (1954), working with a certain line of Brown Leghorns, found that female flocks solicited certain males more than others when such males were presented singly. No quantitative differences in the males' courtship entirely accounted for this. Apart from his study, "preferences" of female flocks for single, unfamiliar males have been ignored, as have the sexual responses of males "visiting" unfamiliar female flocks.

From this brief review, it is apparent that the types of factors effecting non-random mating in wild species can also effect the phenomenon in the Domestic Fowl. However, the exact mode of operation of these factors is largely unknown. Finally, it should be added that its adverse affects on fertility levels renders non-random mating a problem in poultry husbandry also.

Section I

A. Non-random mating behaviour of female flocks with single, 'visiting' males (Situation A)

Material and Methods:

Tests involved B line (Brown Leghorn) birds and Red Junglefowl, all of which had previous heterosexual experience. The individual males and females used in tests were not acquainted. Female flocks were established some considerable time prior to experimentation, and during testing individual males were released singly into such flocks for short periods (15 minutes in the case of the Domestic Fowl, 1 hour in the case of the Junglefowl). Each male was tested twice with each female flock, and male courtship display, female solicitation behaviour, and mating behaviour were recorded. Testing schedules and techniques precluded satiation effects, ensuring that all males and all female flocks involved in any one test received exactly the same treatment. Statistical analysis of results was mainly by the analysis of variance.

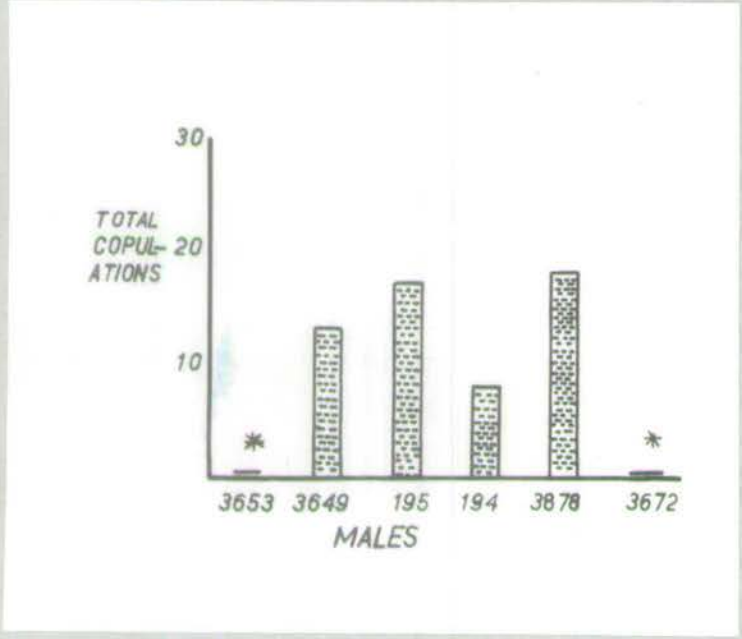
In the B line, four established female flocks were studied. Flocks I and II each consisted of nine adult hens which were tested with each of six own-strain adult cocks; one female had to be excluded at an early stage in the experiment due to ill health. Flocks III and IV each consisted of thirteen hens, and were each tested with twenty-seven own-strain males. Two flocks of Red Junglefowl females (V and VI), each of twelve individuals, were tested with eight conspecific cocks which were otherwise held in an all-male flock.

Results:

The data for flocks I and II were pooled, since females of the two flocks exhibited similar solicitation distributions; a similar procedure was adopted with data from flocks III and IV, but not with data derived from the two junglefowl flocks.

The results for flocks I to IV are given in figure 17. Results for flocks I and II indicated a significant difference in the solicitation frequency of the females to the six males ($p < .01$), and a similarly significant result was obtained for flocks III and IV. A similarly significant non-random distribution of copulation was observed with respect to both pairs of flocks ($p < .01$ in both cases). In neither case was there an overall significant correlation between the distribution of copulation and solicitation; there was, however, a correlation in some respects and of an incomplete nature. Males which were solicited most did not necessarily copulate most, though generally males which were least solicitated copulated least. It was thus apparent that although solicitation distribution exerted a considerable affect on the incidence of copulation, differential male sexual vigour was also important in this respect. Significant correlation between solicitation and copulation distributions was accordingly only seen when a male was solicited very little, or when a "preferred" male was also one of high sexual vigour.

In flock V, crouching of junglefowl hens to the eight cocks was distributed non-randomly ($p < .05$), some cocks


30
TOTAL COPUL- 20
ATIONS
10
*
*
3653 3649 195 194 3878 3672
MALES

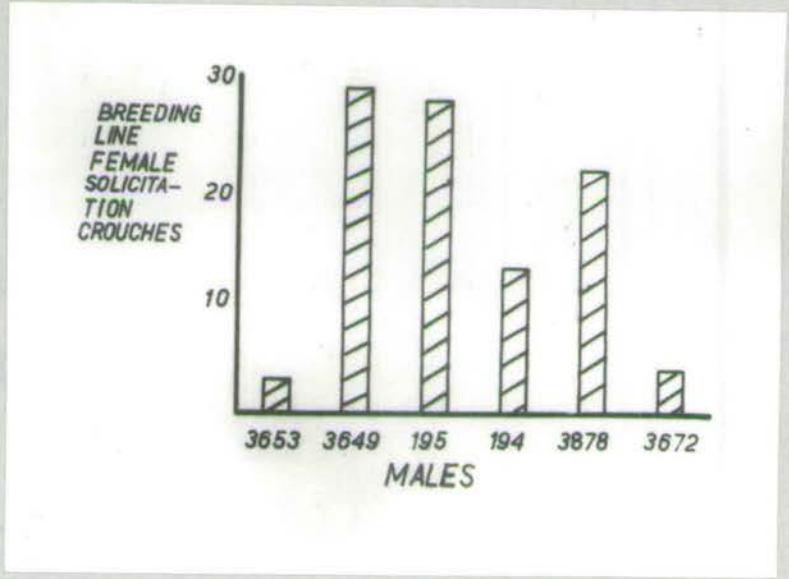
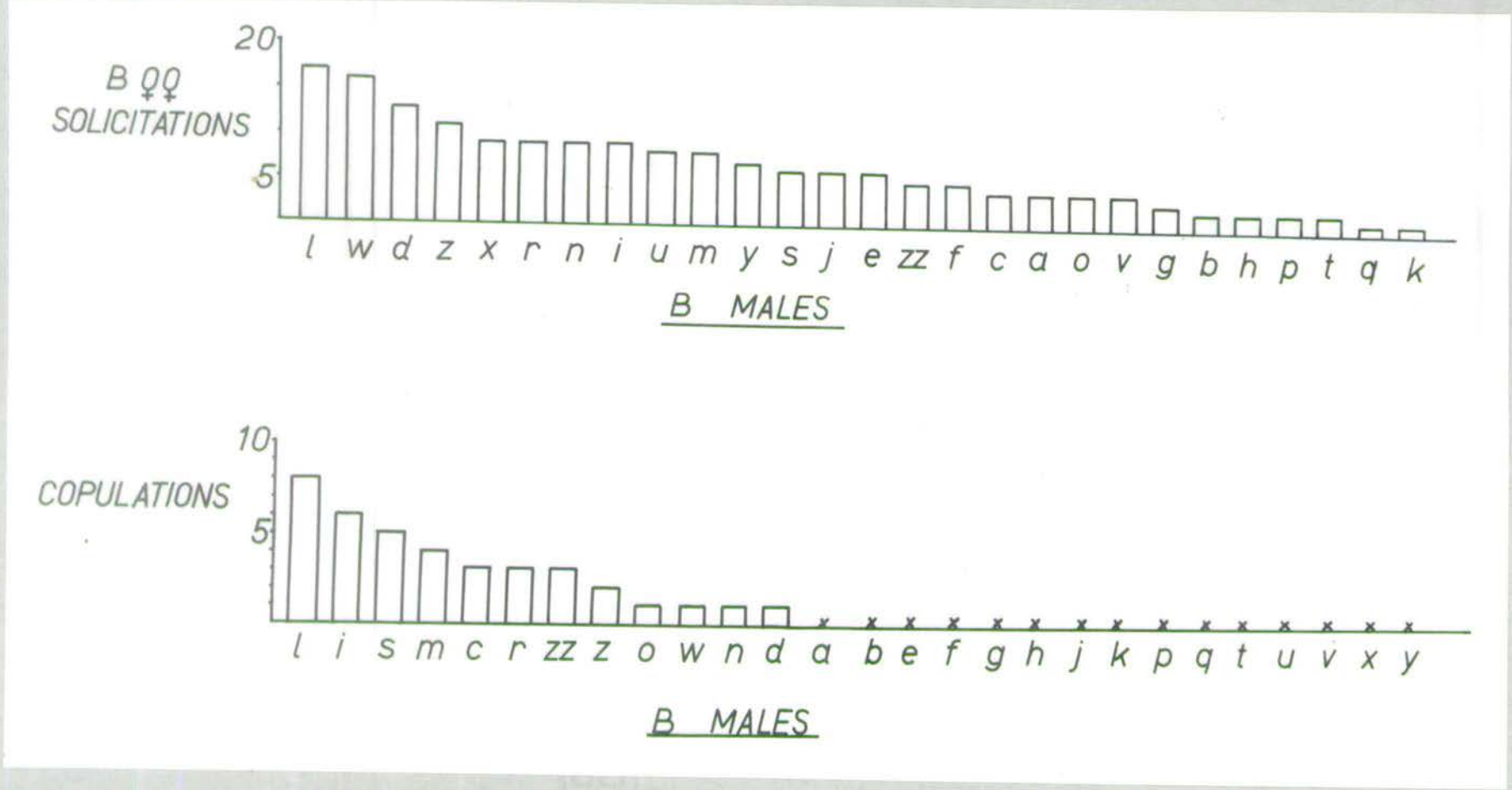

30
BREEDING LINE FEMALE SOLICITA- 20
TION CROUCHES
10
3653 3649 195 194 3878 3672
MALES

Figure 17: Solicitation of and copulation with 'visiting' own-strain males by B line females (Situation A)

Results for flocks I and II above, for flocks III and IV below

X indicates zero reading


20
B ♀♀
SOLICITATIONS
5
l w d z x r n i u m y s j e zz f c a o v g b h p t q k
B MALES
10
COPULATIONS
5
l i s m c r zz z o w n d a b e f g h j k p q t u v x y
B MALES

eliciting more solicitation than others. Copulation distribution was also non-random ($p < .05$), but copulation and solicitation distributions were uncorrelated significantly. Copulation incidence was determined by both the solicitation distribution and differential male sexual vigour. In flock VI, both solicitation and copulation were randomly distributed amongst males, and their distributions uncorrelated. These findings are summarised in table 14 .

Solicitation distribution in the two junglefowl flocks was similar in some respects. Cocks R and BY elicited much crouching in both flocks, and these two males plus male B copulated most in each flock. No overall significant correlation in either solicitation or copulation distributions between the two flocks was observed, however. It is interesting to note that the most solicited male, R, was the alpha male in his home flock of sixteen cocks; no overall correlation between home flock social status and degree of solicitation elicited in flock V was apparent however.

It was apparent from this study that established female flocks of domestic and jungle fowl responded sexually far more to some unfamiliar males than to others. Whether learning is important in this respect or not is not known. In short duration tests marked assortative mating was seen, and female solicitation distribution exerted a considerable, though not absolute, affect on the distribution of copulation. Since non-random mating can have little affect on evolution

TABLE 14

Situation A - Distribution of solicitation and copulation in two Junglefowl flocks (V and VI)

Males	Solicitation Responses		Copulations	
	Flock V	Flock VI	Flock V	Flock VI
R	18	13	11	11
LB	12	2	6	3
BY	9	7	7	9
Y	7	3	6	5
G	7	9	2	6
B	6	7	6	7
W	4	2	1	2
DB	3	3	4	3

or population structure unless it is both prolonged and pronounced, some incidental observations on the stability of the above mentioned type of non-random mating over a seven month period will be described below.

Over a period of seven months, flocks I and II were tested irregularly with all or most of the same six males alluded to above in roughly the same manner as part of other experiments. In all, nine tests were carried out, and the results are given in table 15. . Although there was some variation in the patterns of solicitation and copulation between tests, it was evident that the distributions of copulation and solicitation were not radically altered throughout the testing period. Generally speaking, the most solicited males in the first test remained so throughout the seven month period, and the same cocks copulated most throughout. The inference was that both the stimuli involved in effecting non-random female solicitation and the sexual vigour of individual males remained largely unaltered during the study period. Since these results were derived from what was essentially not a rigorously controlled experiment, it was apparent that non-random mating in Situation A was a fairly stable phenomenon.

B. Non-random mating behaviour of female flocks with single 'resident' males (Situation B)

Material and Methods:

Since some knowledge of this type of non-random mating

TABLE 15

Situation A - Stability of non-random solicitation in Brown Leghorns over seven months

Males	♀♀ crouch responses									♂♂ rank order								
	Jan	Jan	March	March	April	May	May	June	Jly	Jan	Jan	March	March	April	May	May	June	Jly
3649	29	29	18	12	12	12	11	7	6	1	1	1	2	3	1	1	2	3
3878	22	-	15	13	17	11	9	11	15	3	-	2	1	1	2	2	1	1
195	28	24	6	7	15	9	6	5	7	2	2	4	3=	2	3	3	3	2
194	13	15	12	7	10	3	5	4	-	4	3	3	3=	4	4	4	4	-
3672	4	-	2	0	1	0	0	-	-	5	-	5=	4	5	5	5	-	-
3653	3	9	2	-	-	-	-	-	-	6	4	5=	-	-	-	-	-	-
	Copulations									♂♂ rank order								
3649	13	4	8	4	5	7			4	3	1=	2	2=	2	3			3
3878	19	-	12	10	10	11			11	1	-	1	1	1	1			1
195	17	4	5	4	4	9			9	2	1=	3=	2=	3=	2			2
194	8	3	5	4	4	2			-	4	2	3=	2=	3=	4			-
3672	0	-	0	0	0	0			-	5=	-	4=	3	4	5			-
3653	0	0	0	-	-	-			-	5=	3	4=	-	-	-			-

Month of individual tests is indicated. A dash indicates that a bird was not tested. Rank order is an assessment of cocks by no. of crouches elicited or no. of copulations completed. Data on copulation was not recorded in late May and June.

behaviour in chickens already existed in the literature, this study was confined to Red Junglefowl. Flocks V and VI were used in this study, and a single adult male was caged with each flock. Cock X was caged in flock V eighteen days prior to observation, and cock Y in flock VI eleven days prior to observation. Observations of sexual behaviour were made on any one flock on alternate mornings and afternoons, from 09.30 - 12.45 and from 14.00 - 18.15 hours respectively. Flock V was observed on three afternoons and two mornings, flock VI on three mornings and three afternoons. In one flock, the male was removed overnight prior to morning observation and released into the flock when observations commenced, in the other flock the male was never removed.

Females were identified by coloured leg rings. Male courtship activities and mating patterns orientated to specific females were recorded, as was female solicitation behaviour, in order to determine a) whether the distribution of resident males' sexual behaviour amongst females was at random and b) what affect female solicitation exerted on this distribution. Additionally, the female peck-order was determined from the outcome of 295 encounters between females observed prior to and during experimentation in flock V. The purpose of this was to determine whether the hen's social rank affected the degree to which she crouched and was courted and mated.

Results:

Flock V and Cock X

Male sexual activity is summarised in table 16 . Copulation was randomly distributed, and only one solicitation response was not succeeded by male mounting. Cock X forced seven matings, several of which were with hens which were never observed to solicit the male throughout the testing period. Attempted mounting (i.e. unsuccessful attempts to mount an unreceptive hen) was rare and randomly distributed. The distribution of waltzing and intention movements of waltzing (side display) was non-random ($p < .05$), but that of the rear approach was not. An analysis of daily readings showed, however, a significant overall variance in total courtship activities + mounting (which was not crouch-induced) directed to the individual hens ($p < .05$).

The basis of non-random mating in flock V was obscure. There was no overall correlation between female social rank and extent to which they were courted by the cock, but the top-ranking hen, hen C, was courted at a consistantly higher frequency than the other females throughout the experiment. This was probably due to two factors; firstly, she exhibited no great tendency to flee from the displaying male, and this was particularly noticeable when the male waltzed to her. When she failed to move away after male waltzing, the male often waltzed several times to her in rapid succession. Other hens did not behave in this manner, fleeing from the displaying

Male Sexual Activity	♂♂ ♀♀ A	♂♂ ♀♀ B	♂♂ ♀♀ C	♂♂ ♀♀ D	♂♂ ♀♀ E	♂♂ ♀♀ F	♂♂ ♀♀ G	♂♂ ♀♀ H	♂♂ ♀♀ I	♂♂ ♀♀ J	♂♂ ♀♀ K	♂♂ ♀♀ L
Waltz	13	8	12	7	5	1	5	-	9	5	2	12
Waltzing Intention Movements	7	2	22	4	6	3	4	6	-	11	2	5
Rear Approach	12	2	19	10	10	-	9	16	5	5	8	1
Sexual Chase I and II	-	-	-	-	-	-	-	-	-	-	-	-
Attempted Mounting	-	-	-	1	1	-	2	-	1	-	1	1
Mounting - Copulation	-	-	-	-	-	-	-	-	-	-	-	1
Mounting + Copulation	3	-	2	-	3	1	-	1	1	1	-	2
Total Sexual Activity	35	12	55	22	25	5	20	23	16	22	13	22
♂♂ ♀♀ crouches	2	1	1	-	2	-	-	1	1	-	-	1

Table 16: Sexual activity of Cock X in Flock V (Situation B)

male as a rule. Secondly, this hen was spatially isolated from her subordinates for a large percentage of the time during which observations were made, due to their tendency to avoid her. This isolation also stimulates males to display in a vigorous and prolonged manner. The non-random distribution of male courtship activity was not of functional significance, since it was uncorrelated with the distributions of either female solicitation or copulation.

Flock VI and Cock Y

Copulation was not random in as much as only one forced mating was seen, all other matings being stimulated by female solicitation. Cock Y did not copulate with any female which did not crouch to him at some stage during the experiment. The degree to which particular hens crouched and to which they were copulated with were correlated significantly ($p < .05$). Incomplete matings were also restricted in their distribution to those hens which solicited the male. It was evident that the distribution of male mounting and mating behaviour was regulated largely by the distribution of crouching amongst females. Analysis of daily readings indicated a significant overall variance in waltzing (including intention movements) ($p < .01$), some hens eliciting significantly more waltzing than others. The distributions of the rear approach and sexual chasing were random.

Results for flock VI are given in table 17. Considering the findings for both flocks, it is evident that the affect of female crouch distribution on the coition incidence varies according to the sexual vigour of the 'harem' cock. Social organisation of females may exert an indirect affect on the distribution of male sexual behaviour in the present situation. Upp (1928) carried out a similar experiment to that described here with the domestic fowl. His conclusion that male "preference" was involved in effecting non-random mating was unjustified, since he failed to take into account the affect that female behaviour may have exerted on the coition incidence. In his study, hens which remained at a distance from the resident male were mated most, those which remained close to the male were often ignored. In the present study this was not the case, though spatial isolation of the alpha hen from other hens did result in a higher courting frequency to this bird.

C. Non-random mating behaviour of males 'visiting' unfamiliar, female flocks and individuals (Situation C)

Material and Methods:

Two main experiments were carried out in this situation. Experiment a:- Eight B line males were released singly for four-fifteen-minute periods each into an observation pen containing eight marked own-strain females. Observations extended over sixteen days. Female solicitation and male

Male Sexual Activity	♂♂ ♀♀ B	♂♂ ♀♀ BB	♂♂ ♀♀ BL	♂♂ ♀♀ BLBL	♂♂ ♀♀ W	♂♂ ♀♀ WW	♂♂ ♀♀ Y	♂♂ ♀♀ YY	♂♂ ♀♀ G	♂♂ ♀♀ GG	♂♂ ♀♀ R	♂♂ ♀♀ RR
Waltz	18	42	16	40	34	16	15	25	36	12	17	15
Waltz Intention Movement	13	10	3	36	19	4	2	11	34	6	61	17
Rear Approach	10	3	16	8	26	6	16	15	22	9	13	12
Sexual Chase I and II	1	1	2	7	8	-	3	3	3	-	3	2
Attempted Mounting	1	-	4	3	7	-	7	3	6	1	-	2
Mounting - Copulation	-	-	-	-	1	-	1	-	-	-	1	-
Mounting + Copulation	1	-	-	-	3	-	2	-	5	-	3	-
Total Male Sexual Activity	44	56	41	94	98	26	46	57	106	28	108	58
♂♂ crouches ♀♀	1	-	-	-	4	-	1	-	5	-	3	-

Table 17 : Sexual Activity of Cock Y with females of Flock VI (Situation B)

Sexual chase I is with lowered primaries. Sexual chase II is with flapped wings.

mating activities orientated to specific females were recorded. These activities were as follows:-

i) Mounting, trampling and copulating after female crouching.

ii) Attempted mounting (grabbing and chasing, placing a foot on the hen's back).

iii) Rape (complete copulation with an unreceptive female).

iv) Forced interrupted mating (a case of rape terminated prior to actual intromission).

This experiment was designed to analyse non-randomness of the distribution of male mating behaviour in flocks of strange females; this was possible only if the affects of similar non-randomness in female sexual activity were simultaneously analysed.

Experiment b:- It was earlier demonstrated that in heterosexual Junglefowl flocks containing a single, resident male, some aspects of the courtship of the male were non-random in distribution. An experiment was carried out to shed some light on the distribution of male courtship amongst unfamiliar females, and to indicate whether purely morphological differences between hens could be important in effecting a non-random distribution of courtship activities. It is this experiment which is described below.

A group of six B line cocks was tested by simultaneous-presentation three times on a discrimination between two dissimilar own-strain cue females. Cue hen z had a full tail, and a comb flopping to the right of the head, whilst cue hen

zz had a stubby tail, baldish head, slight body moult and a comb deflected approximately thirty degrees to the left. The two cues were intended to simulate to some extent the type of morphological disparity seen between top and low-ranking hens in a female flock. Male courtship behaviour orientated to each cue was recorded, and testing was of such a nature as to preclude satiational and directional affects. Tests lasted ten minutes. Since the cue females were in cages throughout tests, males were not really presented with behaviour cues, simply with morphological stimuli.

Results:

The results for the experiment a, involving release of males into flocks of unfamiliar females, are summarised in tables 18 and 19.

Female solicitation behaviour exerted a powerful affect on male mating behaviour in that males only copulated with hens which crouched to them. Only one case of complete rape occurred. Female receptivity and passivity were apparently necessary for the facilitation of copulation, and when an unreceptive hen struggled as the male attempted to mate with her, this precluded cloacal contact or deterred the male before coitus was achieved. Males did not, however, copulate more with, attempt to mate more with, or have more forced interrupted matings with the females which crouched most to them.

Cocks only copulated with a mean of 39.5 per cent of the females which solicited them. This could not be regarded

MALES	CROUCHES BY FEMALES								TOTAL FOR INDIVIDUAL MALES
	♀♀ ♂♂ 542	♀♀ ♂♂ 349	♀♀ ♂♂ 566	♀♀ ♂♂ 346	♀♀ ♂♂ 559	♀♀ ♂♂ 568	♀♀ ♂♂ 348	♀♀ ♂♂ 541	
I	1	1	3	2	4	2	1	1	15
II	0	2	0	0	0	0	2	0	4
III	0	2	0	1	1	1	0	0	5
IV	0	5	0	3	1	2	1	0	12
V	1	1	3	0	4	0	2	2	13
VI	1	0	0	1	7	4	3	1	17
VII	2	2	3	2	3	2	1	1	16
VIII	1	0	0	1	7	4	3	1	17
TOTAL CROUCHING FOR INDIVIDUAL FEMALES	6	13	9	10	27	15	13	6	99

Table 18 : Crouching by eight Breeding Line hens in response to the courtship of eight Breeding Line cocks (Situation C)

MALES	MALES MATING ACTIVITIES	FEMALES								
		♂♂ ++ 542	♂♂ ++ 349	♂♂ ++ 566	♂♂ ++ 346	♂♂ ++ 559	♂♂ ++ 568	♂♂ ++ 348	♂♂ ++ 541	
I	Percentage female crouches evoking male response (to nearest whole figure)	100	0	66	50	50	100	0	100	
	Copulations (completed)	-	-	1	1	1	2	-	-	
	Att. M. } Male initiated	-	-	1	2	-	-	-	-	
	Rape } mating activities	-	-	1	-	-	-	-	-	
	F.I.M. }	-	-	-	-	-	-	1	-	
II	Percentage etc.	-	0	-	-	-	-	0	-	
	Copulations (completed)	-	-	-	-	-	-	-	-	
	Att. M. }	-	-	-	-	-	-	-	-	
	Rape } Male initiated	-	-	-	-	-	-	-	-	
	F.I.M. } etc.	-	-	-	-	-	-	-	-	
III	Percentage, etc.	-	50	-	100	100	100	-	-	
	Copulations (completed)	-	1	-	1	1	1	-	-	
	Att.M. }	-	-	-	-	-	-	-	-	
	Rape } Male initiated	-	-	-	-	-	-	-	-	
	F.I.M. } etc.	-	-	-	-	-	-	-	-	
IV	Percentage, etc.	-	40	-	33	0	50	100	-	
	Copulations (completed)	-	-	-	-	-	1	-	-	
	Att. M. } Male initiated	-	-	1	3	-	1	-	-	
	Rape } etc.	-	-	-	-	-	-	-	-	
	F.I.M. }	-	-	-	-	-	-	-	-	

(Continued)

MALES	MALES MATING ACTIVITIES	FEMALES							
		♀♀ ++ 542	♀♀ ++ 349	♀♀ ++ 566	♀♀ ++ 346	♀♀ ++ 559	♀♀ ++ 568	♀♀ ++ 348	♀♀ ++ 541
V	Percentage female crouches evoking male response (to nearest whole figure)	100	0	100	-	75	-	100	100
	Copulations (completed)	-	-	3	-	-	-	1	2
	Att. M. } Male initiated	1	-	2	-	-	-	2	-
	Rape } etc.	-	-	-	-	-	-	-	-
	F.I.M. }	-	-	-	-	-	-	-	-
VI	Percentage, etc.	0	-	-	0	71	50	33	0
	Copulations (completed)	-	-	-	-	3	2	-	-
	Att. M. } Male initiated	-	-	-	-	1	1	1	-
	Rape } etc.	-	-	-	-	-	-	-	-
	F.I.M. }	-	-	1	-	-	1	-	1
VII	Percentage, etc.	50	100	100	100	66	50	0	100
	Copulations (completed)	1	1	1	1	-	-	-	1
	Att. M. } Male initiated	-	2	-	-	1	-	-	1
	Rape } etc.	-	-	-	-	-	-	-	-
	F.I.M. }	1	1	1	-	-	-	-	-
VIII	Percentage, etc.	0	-	-	0	71	50	33	0
	Copulations (completed)	-	-	-	-	3	2	-	-
	Att. M. } Male initiated	-	-	-	-	1	1	1	-
	Rape } etc.	-	-	-	-	-	-	-	-
	F.I.M. }	-	-	1	-	-	1	-	1

Table 19 : Mating behaviour patterns of eight Breeding Line males orientated to specific individual hens (Situation C).

as "preference" for certain of the receptive hens, since neither the male group as a whole nor individual cocks copulated significantly more with some hens than others. The percentage of crouching hens copulated with was apparently due to satiation rather than "preference". Cocks did not attempt to mount or have more forced interrupted matings with some hens than with others.

Thus mating behaviour of males was essentially random in its distribution, though, as I pointed out, female solicitation behaviour did exert an affect on male mating activity distribution. Results were essentially similar to those obtained with flocks of Junglefowl in which there were single, resident males.

Table 20 summarises the data derived from simultaneous-presentation tests of six Brown Leghorn males (experiment b). The group as an entity failed to respond significantly differently to the two cue females i.e. courtship display was randomly distributed. But, as table 20 indicates, all males evinced some degree of consistant cue-bias in courtship behaviour, indicating that differences in female morphology may affect the stimulus valency of hens where strange males are concerned. When the sexes are unacquainted, courtship may thus be non-random in distribution, and morphological disparities are potentially important in this respect. Since all males did not show the same type of cue-bias, however, it seems rather unlikely that the type of morphological

TABLE 20

Situation C: Simultaneous-presentation tests of Brown Leghorn males with two morphologically dissimilar own-strain females

Male	Cue $\frac{oo}{++}$ No.Z 7091 ("top")			Cue $\frac{oo}{++}$ No.ZZ7087 ("bottom")		
	Waltzes	Total Courtship Displays	Time Duration (Secs)	Waltzes	Total Courtship Displays	Time Duration (Secs)
a	0	35	1315**	4	42	905
b	25	83	771	59**	126*	1263**
c	36	167**	1268**	20	90	796
d	3	35	644	46**	98**	1511**
e	2	44	692	5	75*	805*
f	15	51	1060**	14	31	704
TOTAL	81	415	5750	148	462	5979

* 1
** 5 % levels of significance (t test) of cue-bias. All measures relate to performance in cage areas surrounding cue cages.

differences extant between top and low-ranking hens would normally be important in effecting non-random male courtship behaviour distribution. That the two cues evoked different response levels in different males is puzzling; either some factor other than morphological ones was involved, which seems unlikely, or past experience of the males was a critical factor.

D. Non-random mating behaviour in heterosexual flocks containing several 'resident' males (Situation D)

The study was conducted with Red Junglefowl, partly in order to compare non-random mating in such situations with that known to occur in the domestic chicken (Guhl, 1962), and partly because it was felt that male dominance relationships are important in effecting non-random mating in wild species, and that they should be further analysed. The experiment was in two parts:-

I) Material and Methods:

A flock of fifteen females and four males was established in a single run, and time allowed for social relationships to become stabilised. The social rank order of the males was determined from the outcome of 373 male encounters observed immediately before and throughout the experimental period, and the social hierarchy proved to be linear thus:-

$$W > Y > R > G$$

Sexual behaviour was observed on three successive afternoons (14.00 - 18.15) and on two successive and a third morning

(09.30 - 12.30). Observations indicated that these observation periods covered the main periods of sexual activity. The extent of my observations was thought to be sufficient to gain an overall impression of the sexual activity during the period of study. Records of male courtship to individual hens (waltzing, the rear approach and sexual chasing) and of completed matings were kept. Any male interference in mating was also noted, and the identity and social rank of the males concerned recorded.

Results:

The results are given in table 21. When the males were ranked according to total sexual activities performed, the ranking was:-

W	343	activities
R	134	"
Y	98	"
G	2	"

Thus a strong correlation between male dominance status and sexual activity was observed, though cock R was somewhat anomalous in this respect. This was due to transitory periods of increased aggression shown by this male, during which it often initiated conflicts with the alpha cock, and even 'won' a few such encounters, without materially altering its social status permanently. In these periods of heightened aggression, R waltzed at an above normal frequency both to the other males and to the females, and a glance at the table

Cock	Waltzes and Intention movements of waltzing	Rear Approaches	Sexual Chasing	Attempted Mounting	Mountings	Completed Matings	Female crouch responses
W (hite)	193	131	-	12	1	6	1
Y (ellow)	10	56	-	27	5	-	-
R (ed)	76	37	1	20	-	-	-
G (reen)	1	-	-	1	-	-	-

TABLE 21

Situation D; Part I; The total recorded sexual activity of the four males in a heterosexual Junglefowl flock

The males are given in order of social dominance.

(21) reveals that it was in this category of courtship behaviour alone that R exceeded its "superior", Y. Only in the case of the rear approach was there an absolute correlation between frequency of performance by males and their dominance status. Social rank and the occurrence of courtship and mating activities were correlated, but not absolutely.

Dominance relationships exerted a further affect on the incidence of copulation through interference with matings. Only the alpha male, W, interfered with subordinates' matings. It precluded other cocks from copulating, interrupting Y on seven occasions and R on two, by direct, overtly aggressive attacks. The hens were unreceptive at this stage in the experiment, and this, added to the effects of dominance status and interference on sexual activity, resulted in non-random mating. Cock W, which copulated six times, was the only male to do so, and remained unmolested during its matings.

2) Material and Methods:

On the completion of the above observations, the flock structure was modified, male G being removed and three strange males being added (WB, BL and B). A sixteen day period was allowed for social relationships to become stabilised and one female died during this period. The structure of the new social hierarchy was then determined from the outcome of 715 male-male encounters. It proved to be of a linear nature:-

$$WB > W > Y > R > BL > B$$

The only instability in social relationships was between B and BL. Subsequently, similar observations of sexual behaviour to those carried out with the above-described flock were made.

Results:

Male sexual activity is given in table 22 . The ranking of males according to total sexual activities performed was as follows:-

W	339	activities
WB	316	"
R	113	"
Y	46	"
B	7	"
BL	2	"

The correlation between male social status and sexual activity was less marked than in the four male situation described above. There was no absolute correlation between the two for any one activity, but broadly speaking, dominant males were more active sexually than lower-ranking ones. Interference was not restricted to the top-ranking male, males R and W also exhibiting interference behaviour. The distribution of interference behaviour among males was not absolutely correlated with social status either. The alpha male interfered with almost every copulation attempt of his subordinates, and the only two completed matings by subordinate males were achieved through the slowness of the alpha male in approaching the treading subordinate male.

Male	Waltzes and intention movements of same	Rear Approaches	Sexual Chases	Attempted Mountings	Mountings	Completed Matings	Female Crouches
WB	178	108	14	6	7	3	1
W	156	141	6	11	24	1+	18
Y	3	30	2	5	5	1	-
R	73	22	13	3	2	-	-
BL	2	-	-	-	-	-	-
B	4	3	-	-	-	-	-

TABLE 22

Situation D, Part 2: The total recorded sexual activity of the six males in the heterosexual Junglefowl flock

The males are listed in order of social dominance.
+ indicates a doubtful instance of actual intromission.

In both cases, the alpha male chased off the subordinate after copulation. WB also interfered in the courtship of subordinates, especially sexual chasing. The top-ranking male in both the four and six-male situations was also observed to react aggressively towards subordinate males when the latter crowed, which may indicate the crowing is associated with territoriality and dominance behaviour.

Interference in the alpha cock's matings by subordinates, unlike the converse phenomenon, did not involve (except in one instance) an overt attack on the treading male. Usually the subordinate males attacked the hen being trodden or attempted to mount her, which latter behaviour often resulted in the dislodgement of the alpha cock prior to intromission. Attacks on the crouching hen were probably due to redirected aggression, because it is well known that domestic fowl will readily attack any conspecific which is fluttering or moving in a rapid and jerky manner. Previous experience with the dominant cock effectively inhibited aggressive responses towards him when he behaved in such a manner during mating, and aggressive behaviour was oriented instead towards the female he was treading.

Cock R did attack cock W during its copulation attempts, and these attacks can be regarded as true social status violations; much of the interference by R took place during periods of intense, general sexual excitement, during which all four top-ranking males were strongly aroused. Inter-

ference by subordinate males was attributable to increased male sexual arousal in the six-male situation, and was reminiscent of the situation described by Scott (1950) in the Prairie Chicken.

Statistically significant non-random mating did not occur, and this was attributable to the less intense mating activity of the dominant male (as opposed to the top-ranking male in the four-male situation) plus the interference by subordinates in many of its copulation attempts. Solicitation was, however, non-random, cock W eliciting 18 out of the 19 observed crouches. The dominant male was thus not solicited most (c.f. Guhl, 1951), but the basis of the observed bias for W in female solicitation is unknown.

It was concluded that increased interference in the six-male situation was attributable to increased sexual arousal through social facilitation. Non-random female solicitation behaviour was not especially related to male social ranking, and would probably only result in non-random mating when the "preferred" male is a) the top-ranking male and b) sexually vigorous and undisturbed during mating. The above results indicate that this last condition is unlikely to pertain in flocks containing even as few as six males. The sexual activity of males was broadly correlated with their social status.

Conclusions

Several points emerging from the foregoing description

of non-random mating behaviour in captive junglefowl and Brown Leghorns should be stressed. It was apparent that in all four experimental situations studied, some aspect of sexual activity was non-random in distribution. Assortative mating occurred in situations A and D. The mechanisms effecting non-random mating and distribution of sexual activity in the two subspecies were essentially similar, and of the same type as those known to operate in many wild bird species. Non-random mating is common in conditions of captivity and domesticity (Smyth, 1962; Hayman, 1964; Allee, 1950), and such conditions may indeed enhance the phenomenon. Nevertheless, there were some striking similarities between the present findings and some of those reported for wild species. Situation D revealed interesting similarities to the mating systems of certain wild, lek-displaying grouse (Tetraonidae). In the Sage Grouse and Prairie Chicken (Scott, 1950), mating is also restricted to one or a few dominant males, which preclude the mating of subordinate cocks. In most of the lek species of grouse, social status violations are also restricted, as they are to a large degree in jungle and domestic fowls, to the moment of attempted copulation. In the Greater Prairie Chicken, the dominant male may be attacked during mating, and a similar phenomenon has been described above in Burmese Red Junglefowl during moments of intense sexual arousal. The present results suggest that in arena-displaying grouse with loosely-organised territorial

behaviour, interference in mating could potentially be an important factor in determining the copulation incidence. Situation D above also resembles that pertaining in many harem species of birds and mammals.

The similarity of non-random mating behaviour and the factors regulating it in Red Junglefowl and Domestic Fowl is not surprising in view of their similar social organisation (Banks, 1956) and social behaviour (Kruijt, 1964) in captivity. Whatever the mating system of wild junglefowl is like, the present study has revealed that the propensities for non-random mating and possibly sexual selection are present.

In some respects it seems advisable in the light of the present findings to discard the terms commonly used in connection with non-random mating, namely "preference" and "preferential mating". In many cases, and the present one is no exception, it is not clear whether non-randomness of sexual behaviour is effected through innate or learned responses to stimuli of differing valencies. But courtship in Domestic and Jungle Fowl is composed largely of signal-response sequences, and the <u>males</u> at least appear to respond to the signals independently of the signaller's identity. Perhaps this could be regarded as 'preference' for particular "personalities" however. Moreover, one casual observation made on a Brown Leghorn male penned singly with a flock of own-strain hens suggests that some caution is required in

determining terminology to be used. This male was resident in the flock for some time and it was noticed that he was persistently reacting in an aggressive manner to one particular female, which he chased and attacked whenever she ventured down from the roost. This behaviour persisted for many weeks, but the male never responded aggressively to other hens in the flock. Since the female did not appear to this observer to differ from other flock-members, it was concluded that the male's behaviour was in fact a learned antipathy. The question arises, "if antipathy, why not preference?" However, since it has been shown above that many factors are involved simultaneously in effecting non-random mating as a rule, whether or not "preference" is involved, it is clear that the term "preferential mating" is no longer tenable.

The above account has indicated something of the mechanisms involved in non-random mating in Junglefowl and Domestic Fowl. In the following section, a more detailed analysis of the mechanisms effecting non-random solicitation of the type observed in Situation A will be presented. This situation was chosen for extensive analysis in view of the most marked assortative mating seen in it, and because it was less evident how non-random mating was effected in this situation than in others. Hens responded far more to some males than to others, but the reason for this was far from obvious, especially since all males appeared extremely

similar in morphology to the human eye.

Section II

An analysis of the factors effecting non-random female solicitation in Situation A

Three types of characteristic having individual distinctness in Brown Leghorns and Red Junglefowl were analysed in order to determine their importance in relation to non-random female solicitation distributions. They were:-

i. Male courtship display

ii. General male morphology

iii. Male courtship vocalisation

A. The importance of quantitative differences in male courtship and of morphological differences:-

a) It was pointed out earlier, that during the testing of flocks I and II, III and IV, and V and VI (Situation A), records of male courtship activity were kept. In the case of the twenty-seven cocks tested with flocks III and IV, thirteen measures of morphology were also taken prior to experimentation. Male comb and wattle hue were classified according to a comparative scale as pale, medium, bright or very bright red, a more objective assessment being impracticable. The comb was further classified as full (undubbed) or dubbed, upright or "floppy". Comb and wattle size were gauged by taking traces of one aspect and measuring trace area by planimetry. Weight was recorded as an indication of relative size, and maximal standing height was read off against a calibrated

scale. All other measures are self-explanatory. Since non-random female solicitation distribution was observed in all three Situation A tests, courtship and morphological data were analysed in order to determine whether the distribution of individual or combinations of such factors amongst males was correlated with the observed pattern of crouching of hens.

Flocks I and II

Details of the courtship of Brown Leghorn hens of both flocks (data pooled) by the six Brown Leghorn males is given in table 23. Some degree of quantitative variability in courtship between males was observed (notably in stamp-squatting and titbitting), but there was no significant correlation between such variability and the female solicitation pattern.

Flocks III and IV

Tables 24 and 25 illustrate the findings. No overall correlations between inter-male variability in single or combinations of factors and female solicitation distribution were observed. Whilst a more elaborate analysis must await the computer, it was apparent that differences between males in the measures taken, whilst considerable in some cases, were not all important in effecting non-random female crouching. It was inferred that either other, unmeasured factors were important, or that the present measures were not subtle enough to detect important differences in the factors

MALE	WALTZ	WING FLAP	TITBIT (HIGH+ LOW INTENSITIES	BODY SHAKE	HEAD SHAKE	AUTO-PREENING	TAIL WAG	BILL WIPE	STAMP+ SQUAT	REAR APPROACH	HIGH STEP	STRUT	NON-SPECIFIC VOCALISATIONS	TOTAL DISPLAY
3653	39	61	49	12	20	1	0	10	20	0	3	1	103	319
3649	54	41	55	14	31	0	0	2	5	19	8	0	38	269
195	63	60	69	12	30	1	0	0	0	27	13	0	66	344
194	42	29	53	7	18	2	0	17	0	11	27	0	89	296
3878	40	30	58	16	72	0	0	0	4	39	19	0	70	359
3672	23	40	136	5	42	6	0	5	0	0	10	0	18	276

Analysis of Situation A: Table 23 - The rate and form of courtship display of the six Breeding Line cocks in Flocks I and II (data pooled).

TABLE 24

Importance of morphological differences between Brown Leghorn males in effecting non-random solicitation by Brown Leghorn hens (Tests of flocks III and IV)

Male	Comb Colour	Comb upright or 'floppy'	Comb size (sq.cms.)	Comb full or dubbed	Wattle colour	Wattles equal or unequal in size	Wattle size (sq.cms.)	Tail size	Mean spur length (inches)	Max. height (inches)	Av. weight (kgs)	Presence and nature of phenotypic irregularities	♀♀ solic-atio respo-es
A	Pale	Upright	7.04	Full	Pale	equal	1.83	Small	10/24	26.5	1.725	3 Black Comb Points	4
B	Medium	Upright	8.22	Full	Medium	Equal	2.51	Medium	17/24	27.0	2.135	1 De-formed wattle	2
C	Bright	Upright	4.48	Dubbed	Bright	Equal	2.71	Full	8/24	25.75	2.085	1 Comb scar	4
D	Bright	Full Flop	9.51	Full	Bright	Equal	3.52	Medium	10/24	28.0	2.190	2 Black comb points	13
E	Bright	Half Flop	8.61	Full	Bright	Equal	3.64	Small	9/24	28.25	2.375	White on 1 wing	6
F	Very Bright	Half Flop	7.83	Full	Very Bright	Equal	2.74	Medium	10/24	27.75	2.400	None	5
G	Bright	Full Flop	9.40	Full	Bright	Equal	3.27	Medium	9/24	28.00	2.170	2 Black comb patches. Some white on wings	3

I	Very Bright	Upright	2.34	Dubbed	Very Bright	Equal	5.12	Medium	14/24	25.00	2.295	White on tail. Deformed and swollen feet	2
I	Very Bright	Upright	1.82	Dubbed	Very Bright	Equal	3.54	Full	17/24	26.00	2.340	None	2
J	Pale	Half Flop	8.85	Full	Pale	Equal	3.45	Medium	20/24	27.00	2.010	None	6
K	Pale	Half Flop	9.10	Full	Medium	Equal	3.90	Small	10/24	27.25	2.304	2 Black comb points	1
L	Very Bright	Upright	2.30	Dubbed	Very Bright	Equal	2.93	Full	19/24	25.00	2.220	Deformed feet	17
M	Very Bright	Upright	2.70	Dubbed	Very Bright	Equal	2.75	Full	14/24	26.00	2.075	White on 1 wing, twisted feet	8
N	Bright	Upright	3.47	Dubbed	Bright	Equal	3.34	Full	12/24	26.00	2.283	White on wings and tail	9
O	Pale	Upright	8.26	Full	Pale	Equal	2.30	Medium	19/24	27.75	2.323	None	4
P	Medium	Slight Flop	10.65	Full	Medium	Unequal	2.05	Medium	16/24	28.00	2.515	White and malformed wing feathers	2

Q	Pale	Slight Flop	10.75	Full	Pale	Equal	2.69	Medium	19/24	26.75	2.220	White on tail	1
R	Bright	Upright	3.33	Dubbed	Bright	Equal	3.10	Medium	14/24	25.75	2.165	White on 1 wing and tail	9
S	Very Bright	Upright	1.98	Dubbed	Very Bright	Equal	2.96	Medium	12/24	25.50	2.345	None	6
T	Medium	Half Flop	8.76	Full	Medium	Equal	2.06	Full	15/24	26.50	2.170	White on both wings	2
U	Medium	Half Flop	7.81	Full	Medium	Equal	2.32	Small	13/24	27.00	2.150	None	8
V	Very Bright	Upright	2.91	Dubbed	Very Bright	Equal	3.25	Medium	11/24	25.50	2.205	White on wings	4
W	Very Bright	Upright	2.28	Dubbed	Bright	Equal	3.20	Medium	21/24	25.25	2.305	White on 1 wing	16
X	Pale	Half Flop	11.15	Full	Medium	Equal	2.74	Medium	22/24	27.25	2.220	Comb scarred	9
Y	Pale	Half Flop	9.25	Full	Medium	Equal	3.05	Medium	18/24	27.50	2.180	None	7
Z	Very Bright	Upright	4.23	Dubbed	Bright	Un-equal	3.80	Full	14/24	27.00	2.485	None	11

ZZ	Very Bright	Upright	3.98	Dubbed	Very Bright	Equal	3.02	Medium	17/24	25.50	2.105	None	5

TABLE 25

Importance of quantitative differences in male courtship in effecting non-random solicitation of females in the B line (Tests of flocks III & IV)

Males	Total Displays	High Intensity Tibbit Duration	Waltz	Rear Approach	High Intensity Tibbit	Non-Specific vocalisations	Wing-Flap	Low intensity Tibbit	Head Shake	Body Shake	Tail-Wag	Bill-Wipe	Auto-Preen	Strutting	High Stepping	Stamp-Squat	Head-Waggle	Sexual Chase	Sieze Neck	Foot on Back	Mount	Trample	Copulate	♀♀ Solicitation Responses
A	126	246	19	0	15	73	4	6	7	0	2	0	0	0	0	0	0	0	0	1	0	0	0	4
B	91	60	0	0	3	69	0	3	12	0	0	3	0	0	0	0	1	0	0	1	0	0	0	2
C	614	842	153	7	86	64	119	36	17	11	0	0	0	14	1	1	1	4	4	2	5	4	3	4
D	588	827	120	1	105	268	52	10	30	0	0	2	0	0	0	0	0	0	0	0	1	1	1	13
E	511	815	52	0	85	218	45	13	26	6	0	6	0	0	0	0	13	0	0	0	0	0	0	6
F	517	270	60	2	49	262	47	17	67	4	0	5	3	0	0	0	1	0	1	1	1	1	0	5
G	129	83	0	0	9	75	6	11	13	0	0	13	0	0	0	2	0	0	0	1	1	0	0	3
H	152	149	1	0	11	34	20	49	18	33	0	16	0	0	0	0	0	0	1	1	0	0	0	2
I	501	1008	96	18	127	94	109	18	28	5	0	0	1	0	0	1	4	0	1	0	7	6	6	9
J	378	133	45	0	18	258	7	18	21	2	0	10	0	0	0	0	0	0	0	1	0	0	0	6
K	273	412	2	1	42	129	56	7	16	5	0	12	0	0	0	3	0	0	0	0	0	0	0	1
L	460	319	38	28	45	140	133	34	37	4	1	0	0	0	0	0	0	0	1	5	16	12	8	17
M	389	445	55	13	47	76	97	41	29	20	2	0	0	2	0	7	0	0	1	0	9	8	4	8
N	402	329	63	14	42	33	191	23	23	9	0	2	0	0	1	1	0	0	1	2	8	4	1	9
O	228	57	10	3	6	136	9	17	18	3	0	25	0	0	0	0	0	1	0	1	1	1	1	4
P	221	97	11	1	12	55	84	36	6	5	2	6	0	0	0	1	2	0	0	0	0	0	0	2
Q	126	11	0	0	1	104	0	1	13	5	1	1	0	0	0	0	0	0	0	0	0	0	0	1
R	721	793	142	0	119	145	227	24	36	9	0	1	6	3	0	1	8	0	3	1	4	3	3	9
S	419	371	80	18	51	73	135	25	25	4	6	0	1	0	0	1	0	0	0	5	6	6	5	6
T	198	109	22	0	12	113	10	6	16	1	0	7	6	0	0	5	0	0	0	0	0	0	0	2

Males	Total Displays	High Intensity Titbit Duration	Waltz	Rear Approach	High Intensity Titbit	Non-Specific vocalisations	Wing-Flap	Low-intensity Titbit	Head Shake	Body Shake	Tail-Wag	Bill-Wipe	Auto-Preen	Strutting	High Stepping	Stamp-Squat	Head-Waggle	Sexual Chase	Sieze Neck	Foot on Back	Mount	Trample	Copulate	♀♀ Solicitation Responses
U	114	152	51	1	13	50	3	2	8	4	1	1	0	0	0	0	0	0	0	2	3	1	0	8
V	372	298	50	8	36	123	129	13	3	5	0	2	1	0	1	0	1	0	1	1	2	1	0	4
W	342	184	54	7	23	116	105	21	13	4	0	0	0	0	0	0	1	0	3	1	5	3	1	16
X	250	98	70	1	14	175	43	26	13	5	0	1	2	0	0	0	0	0	0	1	1	0	0	9
Y	471	261	36	1	32	266	66	11	37	6	2	5	0	1	0	4	4	0	2	2	0	0	0	7
Z	564	467	76	27	62	225	97	32	34	8	0	0	1	1	0	0	1	0	5	9	14	11	2	11
ZZ	373	1485	51	4	115	45	92	16	34	3	0	8	0	0	0	6	0	0	0	2	4	4	3	5

High Intensity Titbit duration given in seconds.
'Total Displays' does not include actual mating activities.

This table should be read in conjunction with the previous one.

examined.

b) An additional test of the importance of comb differences between males was made with Brown Leghorns. The comb is apparently important in individual recognition amongst females (Guhl and Ortman, 1956). Eight males were tested once with each of two established female flocks, each containing ten individuals. Tests lasted fifteen minutes, and male sexual activity and female crouching was recorded. The combs of half the males (experimentals) were then modified by attaching bright red, felt hoods over them (figure 18) in such a manner as to effectively alter comb shape, size, and colour intensity. Four unaltered males acted as controls on retesting.

Crouching was not significantly affected by the modification. There was an 11.1% increase in crouching to control males on retest, and an 18.5% decrease to modified males, but the difference was not significant at the 5% level. The sample size was small. Another experiment involving the dyeing black of male wattles and comb indicated the importance of the comb in sex discrimination, but present results showed that male comb contour and colour intensity are not all important in effecting non-random solicitation. Results substantiated those for tests of flocks III and IV above.

c) Male courtship is clearly important in eliciting female solicitation in both junglefowl and chickens, although solicitation responses do occur unpreceeded by display on

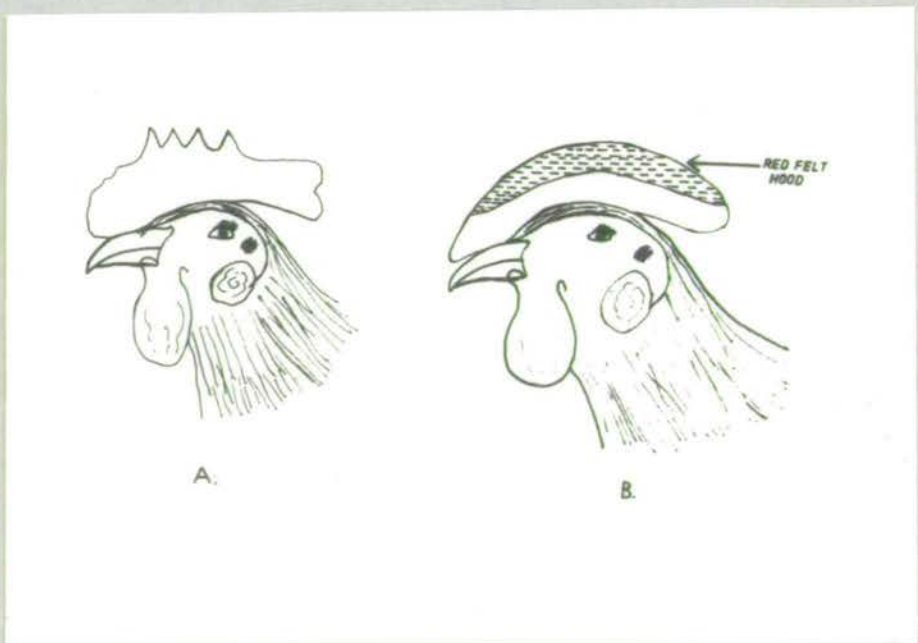

RED FELT
HOOD
A.
B.

Figure 18: Modification of comb shape, size and colour intensity in Brown Leghorn males.

occasions. Experiments reported above evinced no obvious overall correlations between differences in male courtship and the pattern of female solicitation, a finding verifying that of Wood-Gush (1954). Accordingly, it was decided to analyse male courtship from a functional standpoint in order to shed more light on the non-random solicitation problem. In particular, it was felt that patterning of display which was not revealed in analyses described above, could theoretically play an important role in establishing the solicitation pattern.

A sequential analysis of male courtship was undertaken for the Junglefowl test described under Situation A above (page 137), in which non-random solicitation of males by flock V females was observed. The analysis was extended to tests involving both flocks of Junglefowl hens. Single displays immediately preceding female solicitation were analysed, and it was found that out of the total repetoire of fourteen male courtship displays, only six preceded crouching; of these six, only three (Waltz, Rear Approach and Sexual chasing) preceded crouching significantly more than expected by chance (see Table 26). Significant occurrence preceding crouching was based on the assumption that all displays were as likely to precede crouching of females irrespective of their overall occurrence in tests. Despite the lack of correlation between differences in male display and the pattern of female solicitation observed

DISPLAY	Occurrence immediately before crouching	
Waltz	31	
Waltz Intention Movements	8	44
Waltz + Wing Flap	5	
Rear Approach		26
No display before crouching		22
Chase with lowered wings	7	
Chase with flapped wings	3	10
Wing-Flapping		2
Feather-Ruffling		1
TOTAL CROUCHES		105

Table 26: Analysis of male displays immediately preceding crouching of Junglefowl females in Flocks V and VI (Situation A).

Waltz + Wing Flap represents waltzes immediately preceded by wingflapping, which has an 'advertising' or signal affect.

in these tests, it was of interest to note that the most solicited male, R, chased flock V hens significantly more than any other cock, and that three female solicitations of this male were preceded by chasing. R also waltzed forty more times than any other cock in flock V, and performed 242 more courtship activities (including waltzes) than any other male with the same flock.

That factors other than immediately preceding male courtship can effect female solicitation was indicated in these tests by the observation that twenty-two female crouches were not display-preceded, but elicited merely by the proximity of the male. Results pointed to differing signal valencies and functions in the different displays. From the foregoing analysis, it seems possible that differences in the degree of performance of the functionally important displays could have significance in facilitating the expression of non-randomness in female crouching which is based partly upon other differences between males.

A sequential analysis was also undertaken in the B line of Brown Leghorns. Data analysed were derived from observations on thirty-three adult males tested singly for four fifteen-minute periods with each of two flocks of unfamiliar, own-strain hens. All birds had previous heterosexual experience. The analysis was not restricted only to the displays immediately preceding crouching, but also examined the occurrence of displays in pre-solicitation sequences of

TABLE 27

Sequential analysis of display function in Brown Leghorns

Courtship Activity	Overall occurrence in tests	Occurrence immediately preceding ⧺ crouching	% of total occurrence immediately preceding ⧺ crouching	Occurrence in pre-crouch sequences of (up to) three activities	% of total occurrence in pre-crouch sequences
Non-Specific vocalisations	3811	36*	0.9	142*	3.7
Wing Flapping	2147	14	0.6	98*	4.6
Waltzes	1628	85*	5.2	135*	8.3
Titbit (High intensity)	1221	4	0.3	45	3.7
Titbit (Low intensity)	700	4	0.6	17	2.4
Rear Approaches	251	73*	29.1	79*	31.5
Head Shakes	813	1	0.1	21	2.6
Body Shaking	197	1	0.5	10	5.1
Billwiping	160	0	0.0	4	2.5
Stamp + Squat	62	0	0.0	1	1.6
Auto-preening	31	0	0.0	0	0.0
Strutting	22	2	9.1	2	9.1
High Stepping	73	0	0.0	1	1.4
Sexual Chasing	5	0	0.0	0	0.0

* indicates significantly greater occurrence than expected by chance at 1 or 5% levels.

Legend in text.

up to three displays. Significance of occurrence was again judged on the assumption that causation and function were not entirely inter-dependent.

Table 27 gives the results. It was apparent from results that the assumption alluded to above was justified, though interestingly, many of the most performed displays were also of considerable functional significance. Only waltzes, rear approaches and non-specific vocalisations preceded crouching immediately to a degree more than expected by chance. 88.18 per cent of all crouches given after display were preceded by one of these behaviour patterns. These displays will be referred to as crouch-eliciting displays. Some crouches were not immediately preceded by display (voluntary solicitation). The waltz and Rear Approach are also important crouch-elicitors in Junglefowl; sexual chasing was restricted in Brown Leghorn tests by pen size, and vocalisations could not readily be recorded in Junglefowl experiments.

The rear approach was particularly efficacious in eliciting crouching and 29 per cent of rear approaches were succeeded by solicitation. Only 5.2 per cent of waltzes were solicitation-succeeded. The signal efficacy of the rear approach may lie in that it is, unlike waltzing, a sudden quiet approach. The posture of the approaching male is intimidating to the female, but approach is so precipitous that the female has no time to flee. In social interactions

among hens, a subordinate hen when threatened usually flees. When escape is blocked, however, she often adopts a submissive posture, crouching. The situation appears to be the same with regard to the Rear Approach display.

To the present author, non-specific vocalisations appeared to be advertisement displays, drawing the hen's attention to the cock, rather than precipitating solicitation per se. The proximity and physical appearance of the male may be important in eliciting purely voluntary female solicitation, especially early on in a test shortly after the male has been admitted to the flock. If such early call-preceded solicitations are ignored, the occurrence of non-specific vocalisations immediately prior to crouching was not significantly more than expected by chance.

Only one further display, wing-flapping, in addition to the three mentioned above, occurred more than expected in pre-solicitation sequences of up to three displays. An analysis was made to determine whether wing-flapping and non-specific vocalisations were functional in enhancing the crouch-eliciting potential of known crouch eliciting patterns.

Table 28 indicates that only vocalisations, waltzing and high intensity titbitting preceded waltzing more than expected. This was indicative of a causal relationship between titbitting and waltzing and calling and waltzing. However, the crouch-eliciting potential of waltzing was not enhanced by the supposed enhancer displays, since waltzes preceded by supposed

TABLE 28

Potential enhancement of 'waltzing', from a sequential analysis of the courtship of thirty Brown Leghorn males. (844 incidences of waltzing analysed)

	A Courtship Activity of Males	B Occurrence immediately preceding waltzing	C Occurrence immediately preceding crouch-eliciting waltzes	D C/B x 100 (to nearest whole figure)	E % 'enhancer' or 'non-enhancer' preceded waltzes eliciting ♀♀ solicitation
potential 'enhancers'	Non-Specific vocalisations	256*	20	8	6.2
	Wing Flapping	101	2	2	
Supposed 'non-enhancers'	Waltz	196*	13	7	6.8
	Titbit (High intensity	120*	7	4	
	No display	60	6	11	
	Head Shake	43	1	2	
	Titbit (Low intensity	28	4	16	
	Body Shake	5	0	0	
	Bill Wipe	3	0	0	
	Sex Chase	1	0	100	
	Tail Wag	1	0	0	
	Stamp + Squat	1	0	0	

* indicates significantly greater occurrence than expected by chance at 1 or 5% level.

'enhancer' displays and those preceded by 'non-enhancer' displays were not significantly different in their crouch-eliciting potential (see column 4, table 28). Nor did either of these two displays enhance waltzing of themselves. It will be seen from the table, for example, that 16% of waltzes preceded by low intensity titbitting elicited crouching. It is very apparent to the observer that this display does not possess signal value, and it rarely evokes any response in females.

Table 29 summarises data from the investigation of potential enhancement of the rear approach. It was apparent that there was some causal relationship between both wing-flapping and non-specific vocalisations and the rear approach. Moreover, there was some indication of enhancement of rear approach, largely by wingflapping. Wing-flapping frequently graded into the rear approach, and the enhancing properties of this display probably reside in that it advertises the male's presence both visually and acoustically. Wing-flapping also frequently precedes or accompanies crowing in cock Junglefowl and domestic chickens, as well as in many pheasants (e.g. Phasianus colchicus - torquatus). Such wing-flapping is highly stereotyped and possibly to some extent ritualised, especially in Red Junglefowl. It has an obvious signal value, the wings being beaten together above the back to make a loud 'clapping' sound. In non-crowing pheasants, 'wing-whirring' may serve the same advertising

TABLE 29

Potential enhancement of the 'Rear Approach', from a sequential analysis of the courtship of thirty Brown Leghorn males (138 incidences of Rear Approach analysed)

	A	B	C	D	E
	Courtship Activity of Males	Occurrence immediately preceding Rear Approach	Occurrence immediately preceding crouch-eliciting Rear Approaches	C/B x 100 (to nearest whole figure)	% 'enhancer' or 'non-enhancer preceded Approaches eliciting $\frac{oo}{++}$ crouching
'enhancers'	Wing Flapping	60*	18	30	25.3
'enhancers'	Non-Specific vocalisations	31*	5	16	25.3
Supposed 'non-enhancers'	Titbit (High intensity	15	3	20	17.0
Supposed 'non-enhancers'	Head Shake	8	1	12	17.0
Supposed 'non-enhancers'	Waltz	7	1	14	17.0
Supposed 'non-enhancers'	Titbit (Low intensity	7	0	0	17.0
Supposed 'non-enhancers'	Body Shake	4	3	75	17.0
Supposed 'non-enhancers'	Rear Approach	2	0	0	17.0
Supposed 'non-enhancers'	No Display	2	0	0	17.0
Supposed 'non-enhancers'	Strutting	1	0	0	17.0
Supposed 'non-enhancers'	Bill Wipe	1	0	0	17.0

* 1% level of significance

function (e.g. the Silver pheasant). The signal value of wing-flapping is strongest when both visual and acoustic aspects are present, as is the case most often before the rear approach. Vigorous wing-flapping may elicit crouching per se (see table 27). In the Red Junglefowl, wing-flapping may also enhance waltzing and sexual chasing on occasions (see table 26).

Present results suggest that in addition to the overall, general and well-known functions of courtship display, it is possible in the two subspecies of Gallus gallus studied to ascribe specific functions to individual or groups of courtship displays in more detail. A thorough discussion of this aspect of sexual behaviour in the present material must be omitted for the present purposes however.

In conclusion it can be said that differences in male courtship may have some significance in the non-random solicitation phenomenon. If a final detailed solution to this problem is to be forthcoming, however, a more subtle analysis of display than the present one is required. In particular a detailed investigation of patterning of display might repay investigation.

B. The importance of differences in male courtship vocalisation:-

It is proposed simply to describe here an incidental observation made in another connection which may indicate some importance attaching to differences in courtship calls in the effecting of non-random female solicitation. In an earlier

chapter (pages 54 to 57), an experiment was described in the course of which some B line hens were tested with several own-strain cocks before and after they were deafened. An unaltered control flock was used also. Crouching of control and operated female groups to the five cocks before and after operation is given in table 30 . The overall reduction in crouching exhibited by operated hens was not significant ($p > .05$). It should be remembered that tests with own-strain males were interspersed with tests with strange strain cocks. However, the coefficient of variance in crouching was significantly reduced in operates, indicating that the distribution of crouching amongst males was more random after than before surgery. Possibly therefore, vocal cues may be of some significance in the assortative mating phenomenon. Hens used in this experiment were sexually experienced, and the real possibility exists that differences in male vocalisation may be of even greater importance where sexually naive hens are concerned.

Conclusions

It is clear that the mechanism regulating non-random female solicitation of the type seen in Situation A is complex. Patterning of male courtship may be important, and some evidence suggested that differences in courtship vocalisation could be of significance in this respect also. These findings account for the lack of correlation between simple quantitative measures of courtship display and the observed patterns of

TABLE 30

Affect of deafening on non-random solicitation behaviour in Brown Leghorn hens

ale	♀♀ Solicitation responses			
	Controls		Experimentals (Deafened)	
	1st Test	2nd Test	Pre-operation	Post-operation
A	8	2	7	2
A_1	3	7	3	1
A_2	3	4	4	5
A_3	2	1	0	2
A_4	1	3	6	3
TOTAL	17	17	20	13
Coefficient of variance	0.795	0.677	0.685	0.058

female solicitation seen in this study and that of Wood-Gush (1954). Morphological disparities between cocks are not particularly important, though on occasions hens do apparently solicit a male which is not displaying, indicating that factors other than behavioural ones can sometimes elicite the crouch response. Evidence was presented to show that different displays have differing signal functions and values. Further, there may be some functional enhancement of the functionally important displays by certain preceding displays. 'Wing-flapping' particularly appears to possess enhancing value, and this is perhaps not surprising in view of its strong advertising properties and its obvious enhancement of another behaviour pattern, crowing, in another context. Finally, it has become evident that an extensive and elaborate analysis of courtship display from a functional standpoint might well reveal facts of use in analysing non-random solicitation of females in this type of situation.

GENERAL CONCLUSIONS AND DISCUSSION

The experiments described in this chapter have perhaps limited relevance to the problems surrounding the sexual selection phenomenon in wild species. It is clear, however, that non-random mating propensities are present in both subspecies in captivity. This is interesting, since wild Junglefowl seem to bear all the 'hallmarks' of sexual selection, such as conspicuous and well-developed sexual dimorphism, polygamy, and promiscuity. If serious analogies between the

present experiments and situations in nature can legitimately be drawn, the results reported above indicate that both differential female responsiveness (Darwin's "female preference") and inter-male social relationships (which Darwin thought of mostly in terms of actual inter-male combat) could be important in determining the copulation incidence and distribution under harem, lek, or hierarchically-organised group mating regimes. Since such mating system types are probably typical of Junglefowl (Beebe, 1918 to 1922), this chapter may indeed indicate something of how sexual selection actually operates in the ancestral species of Fowl.

Although non-randomly distributed sexual behaviour can occur in males as well as females, its importance is generally thought to be limited with respect to sexual selection. In the present study, some such non-randomness was observed, though it was less marked than that shown by females. Nevertheless, its importance cannot be entirely disregarded though there is little doubt that differential female responsiveness is of greater importance in the sexual selection process.

In previous chapters, non-random mating at inter-breed and inter-strain levels in the chicken was described. It has been demonstrated above that even when individuals bear very close phenotypic resemblance to each other non-random mating can occur. Experiments described in Situations A and D strikingly reveal how non-random mating reduces the effective population size. In experiments with a Junglefowl flock

containing several males and females, only the top-ranking male could have contributed significantly to subsequent generations. Social behaviour and organisation are likely to be of considerable importance in micro-evolution, especially in determining population structure and size. It is evident that many behavioural factors may influence when and where mating takes place. The randomness of mating will be affected by the distribution of female solicitation behaviour, sexual vigour of males and social relationships between and within the sexes amongst other things. It is suggested that further consideration of such factors and their effects could elaborate upon current ideas of population dynamics and micro-evolution.

Previous reference has been made to the similarity between non-random mating mechanisms in present material and some wild animals. This similarity gives added interest to the analysis of non-random female solicitation behaviour. It is clear that the basis of such behaviour is complex, and it would be unrealistic to suggest that the present study has clarified the situation to any great extent. It has underlined the inherent complexity and indicated to some extent those areas in which future research could profitably be conducted. There is no reason to suppose that the phenomenon is less complex in wild species, where territoriality may often be a further complicating factor. It is to be hoped that complexity will not act as a deterrant to future research in

both captive and wild animals exhibiting such behaviour.

General Conclusions

Since fairly thorough discussions have been presented at the end of each chapter, it is intended here only to summarise the main points and ideas emerging from the present work. This work is perhaps best regarded as a model. It was felt at the outset that the potentially important role of behaviour as an evolutionary mechanism or as a factor affecting other evolutionary mechanisms had not received the attention it merited, particularly at the micro-evolutionary level. Thus one of the primary objectives of this work was to elucidate (if only indirectly) the potential role of behavioural factors in evolution below the species level (i.e. of populations). It was felt in particular that this study might shed some light on the feasibility of the micro-evolutionary processes postulated by Sewall Wright (1932).

Secondly, despite the continually growing volume of literature on sexual isolation, there is still a lack of detailed examples amongst vertebrate species. What is needed is knowledge of how sexual isolation operates, of what the underlying mechanisms are like in different animal groups. A model study in a laboratory species facilitates a far greater manipulation of variables, including environment, than is often possible in the field. The utility of this study was enhanced by conducting it upon the Domestic Fowl, comprising as it does so many breeds and strains differing in some characters almost as much as subspecies.

In the introduction to this study, I referred to the emphasis Sewall Wright attached to population size in micro-evolution, and to the difference between apparent and effective sizes. Effective population size is determined by, amongst other things, the sex ratio, the number of fertile animals, and the mating system (Wood-Gush, 1963). An important component of the mating system is social behaviour, and it has been demonstrated here how social behaviour can effect a departure from random mating in a variety of ways. There is no reason to suppose that social behaviour is any less effective in so doing in wild species. Indeed, it is doubtful if a truly random mating system is ever realised in nature. Thus social behaviour may have an important affect on population structure and micro-evolution.

The optimal population structure of a species for rapid evolutionary change is theoretically one in which the population as a whole is split up into partially isolated sub-populations, in which a considerable degree of inbreeding is counterbalanced by limited gene-flow between sub-populations (Wright, loc.cit.). The present study has revealed by analogy something of the feasibility of this model in socially organised species, and especially of the reciprocal relationship between population size and social behaviour, each of which can exert considerable effects on the other.

It has been suggested here that inter-population gene-flow may be restricted in highly social species. What we must

consider is the effective immigrant assimilation rate i.e. the effective genetic contribution made by immigrants to the host population gene-pool. This contribution may be limited by aggressive behaviour on the part of the host population, and gene-flow level in a species may be correlated with the social organisation of the species. Thus in partridges (Jenkins, 1961) there appears to be considerable interchange of individuals between coveys, and there is apparently no social hierarchy within the covey. In chickens (and the same may well be true of other hierarchically and territorially organised species) it has been demonstrated that strangers to a flock are invariably attacked, whether they are of like or unlike phenotype. Such inter-group aggression may effectively preclude effective immigration, as indeed was the case in short-term inter-breed tests with female chickens reported above. There was considerable variability in the "success" of immigrants of like phenotype in entering host populations in the present study also. In the material described here, there was no evidence to suggest that social rank of host population members affected their behaviour towards strangers, but there is some evidence for dogs (King, 1954) showing that rigidity of host population social organisation is correlated negatively with "successful" immigration of strangers.

Other aspects of social behaviour were also demonstrated to exert an affect on effective immigrant assimilation level. Not least of these was the behaviour of immigrants themselves.

Many immigrants of similar phenotype to the host population exhibited aggression on entering the host flock, and even some birds of unlike phenotype which entered in a submissive manner elicited host aggression. It must be borne in mind that assimilation at lower levels in the social structure may not constitute effective assimilation, since such birds may suffer nutritionally, and be restricted by social relationships and reduced 'vigour' from contributing to the reproductive 'output' of the population. It must be presumed that in wild species exhibiting territorial behaviour this type of behaviour will also severely reduce effective assimilation.

It should be pointed out additionally that at just the stage when inter-group gene-flow is thought to be important in micro-evolution, populations will possess the releasers for aggressive behaviour in each other. Despite considerable morphological divergence in breeds of Fowl, it was found that individuals of such breeds readily elicit aggression in one another.

Another type of behaviour which will limit effective population size is non-random mating. In this paper, I have shown that in a 'population' (e.g. strain of chickens or captive group of Junglefowl) in which there is little intra-sexual individual phenotypic variability, marked non-random mating behaviour may occur. Such behaviour may effectively increase the inbreeding coefficient of the population if persistent, and decrease the effective population size. As

WRIGHT has intimated, too great a degree of inbreeding in an isolated population may ultimately lead to deterioration and extinction of the population. Such non-random mating was effected through inter- and intra-sexual social relationships, social experience, and response to relatively slight phenotypic variability. Such non-random mating was shown to have some considerable degree of persistence and stability, and whilst it is true that conditions of captivity may favour the development of this phenomenon, it is also clear that non-random mating may possess similar stability and persistence in some wild species (e.g. Kruijt and Hogan, 1964). Of course, the precise affects that such a mating system have on the evolution of a species depend upon a variety of factors, but it cannot be denied that non-randomness of mating is potentially a significant factor in the evolution of populations.

Finally, with regard to the splitting up of a population into partially isolated units and the maintenance of such partial isolation, positive assortative mating (homogamy) may be an important agent. It was shown that breeds and strains of Fowl, divergent in only a limited number of phenotypic characters, exhibited such behaviour under conditions often exerting considerable bias against its expression. Homogamy was shown to be a fairly stable trait, based upon complex discriminations of plumage colour and other characteristics, and to some extent, especially in females, also dependent upon the nature of the early social environment. Such

behaviour appeared to potentially reproductively isolate breeds and strains, and such may also be true of wild, diverging populations.

It seems possible that some of Wright's theoretical considerations of micro-evolution may require some modification in the light of future ethological research. It is abundantly clear that future considerations of population dynamics must take into account the role of the social behaviour and organisation of the evolving animals.

Potential sexual isolation was demonstrated between breeds and strains of chicken differing little in behaviour. As in other bird species studied, visually-perceived characters possess the most isolating value. Plumage colouration proved to be a, if not the, most important isolating factor, and since it is in this character that most breed and strain distinctness resides, this finding was not unexpected. This was particularly so in Brown Leghorns, in which I showed that the dimorphic plumage colour patterning of the cock was very important in breed discrimination by females. It was also demonstrated that this pattern is enhanced in conspicuousness during lateral display (waltzing) to the hen, and that lateral display is one of the most effective solicitation-eliciting displays in Brown Leghorns and in ancestral Junglefowl. It is not yet entirely clear how discrimination has been affected in breeds bred in such a way that their plumage differs substantially from the 'wild type', though some degree of simplification was noted in

mono-coloured breeds. Nevertheless, homogamy remained at a highly significant level in such breeds. It was observed that homogamy was a weaker trait in males than in females.

The most interesting aspect of homogamy in the Fowl lies in that it is exhibited in the absence of the process known to be important in many precocial birds in orientating sexual behaviour intra-specifically, namely Sexual Imprinting. The cock chicken appears to respond innately to homogamic females, and this response is a strong one even in the absence of potentially reinforcing experience during the juvenile phase. The female is more, if not entirely, dependent upon experience for the normal expression of homogamy as an adult. This situation appears to be the converse of that pertaining in many species of duck (Schutz, 1965), in which it is the female which responds in a largely innate fashion to male releasers. Since females of most duck species are cryptically and similarly coloured, sexual imprinting appears to be a functional necessity in such species. Brown Leghorns are dimorphic in the same respects as most duck species, and it therefore remains far from clear whether this experiental difference in chickens reflects a true species difference or is a by-product of domestication (though this latter seems highly unlikely).

It is now known that so-called Sexual imprinting is not confined to a brief, sharply- delineated, early, critical period (e.g. Hinde, 1962). Nevertheless, in most species which exhibit this type of learning, it characteristically

takes place early in ontogeny, and there is a sensitive period during which the fixation is most readily established. Such a sensitive period may exist for the establishment of homogamy in the Fowl, but it is equally clear that there is no early critical period during which the relevant experience must occur if the trait is to be established. It has been demonstrated that the relevant experience can be witheld until after sexual maturity in females, and homogamy develops just as strongly as in females reared throughout the juvenile phase with own-strain males. Some experience is probably necessary for the full expression as adults of homogamy in both sexes. The function of this experience in males at least seems to be to enhance sexual responsiveness and possibly refine stimulus specificity i.e. it facilitates the expression of an innate response, homogamy.

If aggressive behaviour is to function as an ethological isolating mechanism, a certain amount of generalisation is necessary; that is to say that stimuli eliciting aggressive behaviour must not be so specific that individuals do not possess the appropriate stimuli to release aggressive responses in syntopic relatives. This degree of generalisation exists in the Fowl as illustrated above, though in absolute terms own-breed bias in the orientation of aggressive behaviour in "choice" situations was observed. Sexual behaviour must, on the other hand, be strongly intra-specifically orientated if it is to possess isolating value. Apparently, these two

conditions can be present in a species without there being any fundamental difference in the mechanisms governing the orientation of the two behaviour types, at least in the Fowl. If experience is important in determining the orientation of adult aggressive behaviour, it does not apparently often result in any tendency to flee from or avoid unfamiliar syntopic relatives, and this would be a highly adaptive trait in nature. In the chicken, aggressive behaviour was shown to have considerable isolating potential; only extensive field studies can determine whether it possesses such potential in nature. The value of the present study lies, as previously suggested, in that it has facilitated the analysis of underlying mechanisms of aggressive behaviour orientation, a task not easily tackled in wild species. Whether or not inter-specific aggression can act as an isolating mechanism through the agency of inter-specific territoriality, it is clear that its potential as an isolating mechanism must be temporally restricted to a relatively brief and early evolutionary stage in speciation. (e.g. at the sibling species level).

Non-random mating behaviour is potentially important in one further connection. Sexual selection must be brought about through some kind of non-random mating. Darwin (1871) laid great stress on the importance of female "preference" and inter-male combat as sexual selection mechanisms. It has been shown in this paper that female chickens and Junglefowl often respond sexually more to certain males than others, and that

the net result of such differential responsiveness and differential male vigour may sometimes be non-random mating. Also, social relationships between both males and females may affect the randomness of mating. What is particularly interesting is to examine the way in which such non-random mating operates. It must be conceeded that the present attempt to analyse the basis of what Darwin thought of in terms of female "preference" has produced only a partial solution. It has indicated how complex a phenomenon differential responsiveness of females may be. Variability in solicitation of males may depend upon slight phenotypic differences between such males; in the present case, the patterning of male courtship display appears to be important, whilst morphological differences are probably much less so. Differences in the pitch, tone etc. of vocal courtship 'display' may also be detected and responded to differentially by females. It has been clearly shown how social relationships between males in a heterosexual, multi-male flock of birds with hierarchical social organisation can effect non-random mating. This type of non-random mating system is easier to analyse, since the incidence of copulation is less dependent upon female solicitation behaviour. Inter-male dominance relationships may override the affects of differential female responsiveness, as was noted in one Junglefowl flock in which the second-ranking male was most solicited by the females, but was precluded from mating by the alpha cock. From the present results, this type of

non-random mating behaviour appears likely to lead to a greater degree of sexual selection than that outlined above. Although non-randomly orientated male sexual activity is probably less important in sexual selection in nature than differential female responsiveness, it should not be entirely overlooked. In the present study such non-randomness was observed, though it did not result in marked non-random mating.

Although there is no conclusive demonstration that such non-random mating as has been observed in wild species actually leads to sexual selection, the inference seems justified enough. It is of course difficult to study the affects of sexual selection on population size and genetic structure unless the phenomenon is being observed in a species with a very short life span. But a thorough study of non-random mating in such species may well enable us to assess something of the overall affects on the species of this type of behaviour and of sexual selection, and indicate the relative importance of various facets of social behaviour and organisation in effecting sexual selection.

It remains only to outline further research which could profitably be undertaken along the lines followed in this project; some of the work to be mentioned is in fact in progress, and it is hoped that other aspects can also be followed up in this laboratory. It is intended to continue the study of the role of experience and social environment in homogamy. The main aims of such work will be to determine more fully to what extent the expression of homogamy in adult fowls depends

upon the nature of the ontogenetic social environment, whether any sensitive learning period affect is involved, and the functional significance of sib imprinting and the nature of its underlying mechanisms. In addition, I hope to determine whether reproductive isolation between breeds of fowl and between related gallinaceous species can be reduced or abolished by inter-specific Sexual imprinting. Finally, a study such as the present one would not be complete without an examination of hybrid isolation, and since such a study is not feasible in domestic chickens, it will perhaps be best attempted with inter-specific gallinaceous hybrids. The chief aim of such work would be to determine whether behavioural isolating mechanisms could preclude backcrossing of hybrids with parental species under-going interspecific hybridisation. Such isolating mechanisms may delay or restrict genetic swamping of parental species somewhat under such conditions.

Further research is also needed on the problems of inter-population gene-flow through migration. What is particularly pertinent to micro-evolutionary theory is how the social organisation of species affects emigration and effective immigration. Long-term studies on natural and possibly domestic populations should be designed to determine at what social stratum immigrants generally enter a host population, and how initial entry affects their reproductive and general "fitness". The subsequent reproductive contribution of assimilated immigrants is of interest, as is the affect of immigrant phenotype on

effective assimilation. Such a study could be extended with profit to comparison of wild species with differing types of social organisation, in order to gauge how and to what degree social behaviour can affect gene-flow.

One further point has emerged from the present work, namely the relatively crude and subjective techniques currently existing for the determination of signal value and function of visual components of animal display. Recently, tremendous advances have been made in techniques for analysing acoustic signals, but the 'information' conveyed by visual display presents a far more difficult analytical problem. It is tentatively suggested here that thorough comparative studies of display function in related bird species could be useful in elaborating our knowledge of signal function and 'information content' of signals. By studying, to put it a little naively, how related species "solve" the same or similar communication problems in similar or different ways we might move a little nearer to the evaluation of information transmission by visual signalling in avian species. A detailed study of display function may also help in the evaluation of non-random mating phenomena. The aspect of communication which should be studied is not so much the signal which is given, but that part (or parts) of the signal which is received and the response evoked in the "receiver".

Acknowledgements

Many persons have been of assistance during the course of this work. In particular my thanks are due to the following:-

My wife, Chris; Dr. D.G.M. Wood-Gush; Dr. A. Manning; Prof. Dr. G.P. Baerends; Dr. J.P. Kruijt; Dr. P.E. Lake; Dr. A. McFarquhar; Mr. L. Thompson; the staff of the P.R.C. Outstation (Milton Bridge); and the Agricultural Research Council.

Literature cited

Allee, W.C. (1950). Dominance and hierarchy in societies of vertebrates. - In: Colloques internationaux du Centre Nationel de la recherce scientifique. 34, Structure et Physiologie des sociétees animales. Ed. P. Grassé, p. 157-181.

Allee, W.C., Emerson, A.E., Park, O., Park, T., and Schmidt, K.P. (1949). Principles of Animal Ecology.

Armstrong, E.A. (1947). Bird Display and Behaviour - Lindsay Drummond, London.

Baerends, G.P. (1958). Comparative methods and the concept of homology in the study of behaviour. - Extrait des Arch. Néerl. de Zool., 13, p.401-417.

Baerends, G.P., and Baerends-Van Roon, J.M. (1950). An introduction to the ethology of Cichlid fishes. - Behaviour Suppl. 1.

Banks, E.M. (1956). Social Organisation in Red Junglefowl hens (Gallus gallus subsp.). - Ecology, 37, p.239-248.

Beale, T. (1839). The Natural History of the sperm whale ... to which is added a sketch of a South-Sea whaling voyage, 2nd Edition, London.

Beebe, W. (1918-22). Monograph of the Pheasants, 4 vols, London.

Blair, W.F. (1954). Tests for discrimination between four subspecies of deer-mice (Peromyscus maniculatus). - Texas Jour. Sci., 6, p.201-210.

Blair, W.F. (1953). Experimental evidence of species discrimination in the sympatric species, Peromyscus truei and P. nasutus. - Amer. Nat., 87, p.103-105.

Blair, W.F. and Howard, W.E. (1944). Experimental evidence of sexual isolation between three forms of mice of the cenospecies Peromyscus maniculatus. - Contr. Lab. Vert. Biol., 26, p.1-19.

Blair, W.F. and Littlejohn, M.J. (1960). Stage of speciation of two allopatric populations of chorus frogs (Pseudacris). - Evolution, 14, p.82-87.

Blest, A.D. (1961). Chapter on Ritualisation in Current Problems in Animal Behaviour, Ed. Thorpe, W.H. & Zangwill, O.L., Univ. Press, Cambridge, England.

Bogert, C.M. (1960). The influence of sound on the behaviour of Amphibians and Reptiles, in Animal Sounds and Communication, Ed. Lanyon, W.E. and Tavogla, Washington.

Bruce, H.M. (1959). An exteroceptive block to pregnancy in the mouse. - Nature, 184, p.105.

Bruce, H.M. and Parkes, A.S. (1960). Role of olfactory sense in pregnancy block by strange males. - Science, 131, p.1526.

Collias, N.E. and Collias, E.C. (1956). Some mechanisms of family integration in ducks. - Auk, 73, p.378-400.

Cooch, F.G. and Beardmore, J.A. (1959). Assortative mating and reciprocal difference in the Blue-Snow Goose complex. - Nature, 183 p.1833-1834.

Crane, J. (1941). Crabs of the genus Uca from the West Coast of Central America. - Zoologica, 26, 145-208.

Crawford, R.D. and Smyth, J.R. Jnr. (1964). Social and Sexual Behaviour as related to plumage pattern in the Fayoumi Fowl. - Poult. Sci., 43, p.1193-1199.

Cushing, J.E. (1941). Non-genetic mating preferences as a factor in evolution. - Condor, 43, p.233-236.

Darwin, C. (1871). The descent of Man, Murray, London.

Denenberg, V.H. and Banks, E.M. (1962). Techniques of Measurement and Evaluation, in The Behaviour of Domestic Animals, Ed. E.S.E. Hafez, Bailliere, Tindall and Cox, London.

Dilger, W.C. (1956). Hostile behaviour and reproductive isolating mechanisms in the avian genera Catharus and Hylocichla. - Auk, 73, p.313-353.

Dobzhansky, Th. (1951). Genetics and the origin of species, N.Yk., 3rd Edtn.

Dobzhansky, Th. (1937). Genetic nature of species differences. - Amer. Nat., 71, p.404-420.

Douglis, M.B. (1948). Social factors influencing the hierarchies of small flocks of the domestic hen: Interactions between resident and part-time members of organized flocks. - Physiol. Zool., 21, p.147-182.

Durietz, G.E. (1930). The fundamental units of biological taxonomy. - Svensk. Bot. Tidskrift, 24, p.333-428.

Errington, P.L. and Hamerstrom, F.N. (1936). The northern Bobwhite's winter territory. - Agr. Exp. Iowa State Coll. Agr. and Mech. Arts. Research Bull., 201, p.302-443.

Evans, L.T. (1961). An interpretation of turkey courtship. - Amer. Zool., 1, p.353.

Fabricius, E. (1962). Some aspects of imprinting in birds. - Symp. Zool. Soc., Lond., 8, p.139-148.

Fabricius, E. (1951). Zur Ethologie junger Anatiden. - Acta. zool. fenn. 68, p.1-175.

Fisher, A.E. and Hale, E.B. (1956). Stimulus determinants of sexual and aggressive behaviour in male Domestic Fowl. - Behaviour, 10, p.309-323.

Fisher, James. (1965). Interspecific Aggression, in the Natural History of Aggression, Ed. Carthy, J.C. and Ebling, F.J., Acad. Press.

Fisher, R.A. (1930). The Genetical Theory of Natural Selection, Oxford.

Geis, A.D. and Elbert, L.H. (1956). Relation of tail length of cock Ring-Necked Pheasants to harem size. - Auk, 73, p.289.

Gilliard, E.T. (1963). The Evolution of Bowerbirds. - Sci. Amer., August, p. 38-46.

Godfrey, J. (1958). The origin of sexual isolation between bank voles. - Proc. Roy. Phys. Soc., 27, p.47-55.

Goodwin, D. (1958). The existence and causation of colour preferences in the pairing of Feral and Domestic pigeons. - Bull. Brit. Ornith. Club., 78, p.136-139.

Gottlieb, G. (1965). Imprinting in relation to parental and species identification by avian neonates. - J. Comp. Physiol. Psychol., 59, p.345-356.

Gray, P.H. (1961). The releasers of imprinting:differential reactions to colour as a function of maturation. - J. Comp. Physiol. Psychol., 5, p.597-601.

Gudmundson, F. (1932). Beobachtunger an isländischer Eiderenten (Somateria m. mollissima). - Sonderdruck aus Beiträge zur Fontpflanzungsbiologie der Vögel, 8, p.85-97.

Guhl, A.M. (1962). The Behaviour of Chickens, in The Behaviour of Domestic Animals, Ed. Hafez, E.S.E., Bailliere, Tindall and Cox, London.

Guhl, A.M. (1953). Social behaviour of the Domestic Fowl. - Tech. Bull. Ag. Exp. Stn., Kansas State Coll., 73.

Guhl, A.M. (1951). Measureable differences in mating behaviour of cocks. - Poult. Sci., 30, p.687-693.

Guhl, A.M. (1942). Social discrimination in small flocks of the common domestic fowl. - J. Comp. Psychol., 34, p.127-148.

Guhl, A.M., Collias, N.E. and Allee, W.C. (1945). Mating behaviour and the social hierarchy in small flocks of White Leghorns. - Physiol. Zool., 18, p.365-390.

Guhl, A.M., and Allee, W.C. (1944). Some measurable effects of social organisation in flocks of hens. - Physiol. Zool., 17, p.320-347.

Guhl, A.M., and Ortman, L.L. (1953). Visual recognition in chickens. - Condor, 55, p.287-298.

Guiton, Philip. (1962). The development of Sexual Responses in the Domestic Fowl, in relation to the concept of Imprinting. - Symp. Zool. Soc. Lond., 8, p.227-234.

Guiton, Philip. (1959). Socialisation and Imprinting in Brown Leghorn chicks. - Anim. Behav., 8, p.26-34.

Gullion, G.W. (1962). Organisation of Quail coveys. - Condor, 5, p.402-415.

Hale, E.B. (1957). Breed recognition in the Social Interactions of Domestic Fowl. - Behaviour, 10, p.240-254.

Hale, E.B. (1953). Social factors in sexual behaviour of turkeys. - Pa. Agric. expt. Sta. Prog. Rept., 108, 4pp.

Hamilton, W.J. and Orians, G. (1965). Evolution of brood parasitism in altricial birds. - Condor, 67, p.361-387.

Haskell, P.T. (1957). Stridulation and associated behaviour in certain Orthoptera. I. Analysis of the stridulation of, and behaviour between males. - Brit. Jour. Anim. Behav., 5, p.139-148.

Haskins, C.P. and Haskins, E.F. (1950). Factors governing sexual selection as in isolating mechanism in the poeciliid fish Lebistes reticulatus. - Proc. Nat. Acad. Sci., 36, p.464-476.

Haskins, C.P. and Haskins, E.F. (1949). The role of sexual selection as an isolating mechanism in three species of poeciliid fishes. - Evol., 3, p.160-170.

Hayman, R.H. (1964). Exercise of mating preference by a merino ram. - Nature, 203, p.160.

Heinroth, O. (1911). Beiträge zur Biologie, namentlich Ethologie und psychologie der Anatiden. - Verh. v. Int. Orn. Kongr., Berlin (1910), p.589-702.

Heuser, (1916). cited in Guhl (1942).

Hilgard, E.R. (1957). Introduction to Psychology, N.Yk.

Hinde, R.A. (1962). Some aspects of the imprinting problem. - Symp. Zool. Soc. Lond., 8, p.129-138.

Hinde, R.A. (1959). Behaviour and Speciation in birds and lower vertebrates. - Biol. Rev., 34, p.85-128.

Hogan-Warburg, A.J. (1964). The courtship of the Ruff, Philomacus pugnax (L.). - Arch. Neerl. de Zool., 16, p. 149-171.

Hogben, L. (1946). An introduction to mathematical genetics, Norton, N.Yk.

Hubbs, C.L. (1961). Isolating mechanisms in the speciation of fishes. - in Vertebrate Speciation, Ed. Blair, W.F., Univ. Texas Press, Austin, p.5-23.

Hunsaker, D. (1962). Ethological isolating mechanisms in the Sceloporus torquatus group of lizards. - Evoln., 16, p.62-74.

Hutt, F.B. (1949). Genetics of the Fowl, McGraw-Hill, N.Yk.

Huxley, J.S. (1942). Evolution, the modern synthesis, Allen and Unwin, London.

Huxley, J.S. (1938). The present standing of the theory of Sexual Selection, in Evolution, Ed. de Beer, G., Oxford.

Immelmann, K. (1959). Experimentelle Untersuchunger über die biologische Bedeutung antspezificher Merkmale beim Zebrafinken (Taeniopygia castanotis Gould). - Z Jahrbücher Syst., 86, p.437-592.

Jacobs, W. (1953). Verhaltungsbiologische Studien an Feldheuschreken. - Z. Tierpsychol., 10, p.154-161.

Jenkins, D. (1961). Social behaviour in Partridge, Perdix perdix. - Ibis, 103, p.155-188.

Johnson, N.K. (1963). Biosystematics of sibling species of flycatchers in the Empidonax hammondii - oberholseri - wrighti complex. - Univ. Calif. Publ. Zool., 66, p.79-238.

King, J.A. (1954). Closed social groups among domestic dogs. - Proc. Amer. Phil. Soc., 98, p.327 et seq.

Klopfer, P.H. (1962). Behavioural aspects of Ecology, Prentice-Hall, Englewood Cliffs, N.Jersey.

Knight, G.R., Robertson, A. and Waddington, C.H. (1956). Selection for sexual isolation within a species. - Evoln., 10, p.14-22.

Konishi, M. (1963). The role of auditory feedback in the vocal behaviour of the Domestic Fowl. - Z. Tierpsychol., 20, p.349-367.

Kruijt, J.P. (1964). Ontogeny of social behaviour in the Burmese Red Junglefowl (Gallus gallus spadiceus Bonnaterre).- Behaviour Suppl., 12, p.1-201.

Kruijt, J.P. and Hogan, J.A. (1964). Organisation of the lek in Black Grouse. - Arch. Neerl. de Zool., 16, p.155-157.

Lanyon, W.E. (1959). The behavioural, ecological and morphological characteristics of two populations of alder flycatcher, Empidonax traillii (Audubon). Review of article by R. Stein. - Auk, 76, p.110-111.

Levine, L. (1958). Studies on sexual selection in mice. I. Reproductive competition between albino and black-agouti males. - Amer. Nat., 92, p121-26.

Liley, R. (1962). Some aspects of reproductive isolation in four sympatric species of poeciliid fishes. - Anim. Behav., 10, p.387-388.

Lill, Alan and Wood-Gush, D.G.M. (1965). Potential ethological isolating mechanisms and assortative mating in the Domestic Fowl. - Behaviour, 25, p.16-44.

Lorenz, K. (1964). Ritualised fighting, in The Natural History of Aggression, Ed. Carthy, J.C. and Ebling, J.F., Acad. Press.

Lorenz, K. (1950). The comparative method in studying innate behaviour patterns. - Symp. Soc. Expt. Biol., 4, p.221-268.

Lorenz, K. (1941). Vergleichende Bewegungstudien an Anatinen.- J. fur.Ornithol., 89, p.19-29.

Lorenz, K. (1935). Der Kumpan in der umwelt des vogels. - J. fur.Ornithol., 83, p.213 and 289-413.

Long, E. and Godfrey, G.F. (1952). The effect of dubbing, environmental temperature, and social dominance on mating activity and fertility in the domestic fowl. - Poult. Sci., 31, p.665-673.

Lumsden, H.G. (1961). The display of the Capercaillie. - Brit. Birds, 54, p.257-272.

Maier, R.A. (1962). The role of the dominance-submission ritual in social recognition of hens. - Anim.Behav. 12,p.59.

Manning, A. (1959). The Sexual isolation between Drosophila melanogaster and D. simulans. - Anim. Behav., 7, p.60-65.

Mayr, E. (1963). Animal Species and Evolution, Harvard Univ. Press, Cambridge Massachusetts.

Mayr, E. (1950). The role of antennae in the mating behaviour of female Drosophila - Evoln., 4, p.149-154.

McBride, G. (1964). Social discrimination and subflock structure in the domestic fowl. - Anim. Behav.,12, p.264-267.

McBride, G. (1963). A General Theory of Social Organisation and Behaviour. - Univ. of Queensland Press, St. Lucia.

McCarley, H. (1964). Ethological isolation in the cenospecies Peromyscus leucopus. - Evoln., 18, p.331-332.

Miller, A.H. (1953). A hybrid woodpecker and its significance in speciation in the genus Dendrocopos. - Evoln., 9, 317-321.

Moody, P.A. (1961). Introduction to Evolution, Harper and Row, N.Yk.

Morris, D. (1956). The feather postures of birds and the problem of the origin of social signals. - Behaviour, 9, p.75-113.

Murchison, C. (1935a). Experimental measure of a social hierarchy in Gallus domesticus. I. The direct identification and direct measurement of social reflex No.1. and social reflex No.2. - J. gen. Psychol., 12, p.3-39.

Murchison, C. (1935b). II. Identification and inferential measurement of social reflex No.1. and social reflex No.2. by means of social discrimination. - J. Soc. Psychol., 6, p.3-30.

O'Donald, P. (1960a). Inbreeding as a result of imprinting.- Heredity, 15, p.79-85.

O'Donald, P. (1960b). Assortative mating in a population in which two alleles are segregating. - Heredity, 15, p.389-396.

O'Donald, P. (1959). Possibility of assortative mating in the Arctic Skua. - Nature, 183, p.1210.

Orians, G.H. and Willson, M.F. (1964). Interspecific territories of birds. - Ecology, 45, p.736-745.

Parker, J.E. (1961). Observations on the low fertility problem in Cornish Cockerels. - Poult. Sci., 40, p.1214-1219.

Parker, J.E., McKenzie, F.F., and Kempster, H.L. (1940). Observations on the sexual behaviour of New Hampshire males. - Poult. Sci., 19, p.191-197.

Patterson, J.T. (1942). Isolating Mechanisms in the genus Drosophila. - Biol. Symp., 6, p.271-287.

Patterson, J.T., and Stone, W.S. (1952). Evolution in the genus Drosophila, Macmillan, N.Yk.

Pearce, S. (1960). An experimental study of sexual isolation within the species Drosophila melanogaster. - Anim.Behav., 8, p.232-233.

Peckham, G.W. and Peckham, E.G. (1889). Observations on sexual selection in spiders of the family Attidae. - Occ. Papers. Nat. Hist. Soc. Wis., 7, p.1-60.

Peckham, G.W. and Peckham, E.G. (1890). Additional observations on sexual selection in spiders of the family Attidae. - Ibid, 2, p.115-151.

Perdeck, A.C. (1957). The isolating value of specific song patterns in two sibling species of grasshoppers (Chorthippus brunneus Thunb. and C. biguttulus L.). - Behaviour, 12, p.1-75.

Pettingill, O.S. Jnr. (1959). King Eiders mated with common Eiders in Iceland. - Wilson Bull., 71, p.205-207.

Philips, A.G. (1919). Preferential Mating in Fowls. - J.A.A. of I. and I. in Poult. Husb., 5, 28-32.

Popham, E.J. (1947). Ecological studies of the mating habits of certain species of Corixidae and their significance. - Proc. Zool. Soc. Lond., 116, p.692-706.

Potter, J.H. (1949). Dominance relations between different breeds of domestic hens. - Physiol. Zool., 22p. 261-280.

Potter, J.H., and Allee, W.C. (1953). Some effects of experience with breeds of Gallus gallus on behaviour of hens towards strange individuals. - Physiol. Zool., 26, p.147-161.

Rand, A.L. (1949). Glaciation as an isolating factor in speciation. - Evoln., 2, p.314-321.

Riesen, A.H. (1947). The development of visual perception in man and chimpanzee. - Science, 106, p.107-108.

Rivas, L.R. (1964). A reinterpretation of the concepts "sympatric" and "allopatric", with proposal of the additional terms "syntopic" and "allotopic". - Syst. Zool., 13, p.42-43.

Rowley, I. (1965). The reaction of the Superb Blue Wren Malurus cyaneus to models of the same and closely related species. - Emu, 63, p.207-214.

Schjelderup-Ebbe, Th. (1923). Weitere Beiträge zur social und individual Psychologie des Haushuhns. - Z. Psychol., 92, p.60-87.

Schleidt, W.M. (1964). Uber die Spontaneitat von Erbkoordinationen. - Z. fur Tierpsychol., 21, 235-256.

Schleidt, W.M. (1961). Operative Entfernung des Gehörogans ohne Schädigung angrenzender Labyninthteile bei Putenkuken. - Experientia, 17, p.464-465.

Schmalhausen, I.I. (1949). Factors of Evolution, Philadelphia.

Schooland, J.B. (1942). Are there any innate tendencies? - Genet. Psychol. Monog. 25, p.219-287.

Schutz, F. (1965). Sexuelle Prägung bei Anatiden. - Z. fur. Tierpsychol., 22, p.50-103.

Schwartzkopff, J. (1949). Über Sitz und Leistung von Gehör und Vibration-Ssinn bei Vögeln. - Z. vgl. Physiol., 31, p.527-608.

Scott, J.P. and Fredericson, E. (1951). The causes of fighting in mice and rats. - Physiol. Zool., 24, p.273-308.

Scott, J.W. (1950). A study of the phylogenetic or comparative behaviour of three species of grouse. - Ann. New. Yk. Acad., Sci., 51, p.1062-1073.

Selander, R.K. (1965). On mating systems and sexual selection.- Amer. Nat., XCIX, p.129-141.

Selander, R.K. and Giller, D.R. (1961). Analysis of sympatry of Great-tailed and Boat-tailed Grackles. - Condor, 63, p.29-86.

Senden, M.V. (1932). Raum-und Gestaltaufassung bei operienten Blind-geborenen von und nach der Operation, Leipzig, Barth.

Sibley, C.G. (1961). Hybridisation and Isolating mechanisms, in Vertebrate Speciation, Ed. Blair, W.F., Univ. Texas Press.

Sibley, C.G. (1961). Hybridisation in birds: Taxonomic and evolutionary implications. - Bull. Brit. Orn. Club., 79, p.154-158.

Sibley, C.G. (1957). The evolutionary and taxonomic significance of sexual dimorphism and hybridisation in birds. - Condor, 59, p.166-191.

Sibley, C.G. and Short, L.L. Jnr. (1959). Hybridisation in some Indian bulbuls (Pycnonotus cafer x P. leucogemys). - Ibis, 101, p.177-182.

Silson, R.G. (1963). Assortative mating in producing new species. - Nature, 197, p.105.

Skard, A.G. (1937). Studies in the psychology of needs: observations and experiments of the sexual needs of hens. - Acta. Psychol., 2, p.175-232.

Smith, N.G. (1964). Evolution of some arctic gulls (Larus): A study of isolating mechanisms. - Dissert. Abst., 24, p.3901.

Smith, S.G. (1954). A partial breakdown of temporal and ecological isolation between Choristoneura species (Lepidoptera: Tortricidae). - Evoln., 8, p.206-224.

Smyth, J.R. Jnr. (1962). Cited in chapter 18 of The Behaviour of Domestic Animals, Ed. Hafez, E.S.E., Bailliere, Tindall and Cox, London.

Snow, D.W. (1962). A field study of the Black and White Manakin, Manacus manacus, in Trinidad. - Zoologica, 47, p.65-104.

Spieth, H.T. (1952). Mating behaviour within the genus Drosophila (Diptera). - Bull. Amer. Mus. Nat. Hist., 99, p.395-474.

Stalker, H.D. (1942). Sexual isolation studies in the species complex Drosophila virilis. - Genetics, 27, p.238-257.

Standfuss, M. (1896). Handbuch der palÆarktischen Grosschmeltenlinage für Forscher und Sammler, G. Fischer, Jera.

Stokes, A.W. (1961). Voice and social behaviour of the Chukar partridge. - Condor, 63, p.111-127.

Sumner, E.L. Jnr. (1935). A life history study of California Quail, with recommendations for its conservation and management. - Calif. Fish and Game., 21, p.167-256 and 275-342.

Taylor, K.F. and Sluckin, W. (1964). Flocking of domestic chicks. - Nature, 201, p.108-109.

Thompson, H.V. and Worden, A.N. (1956). The Rabbit, New Naturalist monographs, London.

Thorpe, W.H. (1951). The learning abilities of birds. - Ibis, 93, p.252-296.

Tinbergen, N. (1963). On aims and methods of ethology. - Z. für Tierpsychol., 20, p.410-433.

Tinbergen, N. (1959). Comparative studies of the behaviour of gulls (Laridae); a progress report. - Behaviour, 15, p.1-70.

Tinbergen, N. (1951). The study of Instinct, Oxford Univ. Press, Oxford, England.

Tindell, D. and Craig, J.V. (1959). Effects of social competition on laying house performance in the chicken. - Poult. Sci., 38, 95-105.

Upp, C.W. (1928). Preferential mating of fowls. - Poult. Sci., 7, p.225-232.

Vanderplank, F.L. (1948). Experiments in crossbreeding tsetse flies (Glossina species). - Ann. Trop. Med. Parasit., Liverpool, 42, p.131-152.

van Someren, V.D. (1958). A bird watcher in Kenya, Oliver and Boyd, Edinburgh.

Walker, T.J. (1957). Specificity in the response of female tree crickets (Orthoptera, Gryllidae, Oecanthinae) to calling songs of the males. - Ann. Ent. Soc. Amer., 50, p.626-636.

Warren, D.C. and Kilpatrick, L. (1929). Fertilisation in the Domestic Fowl. - Poult. Sci., 8, p237-256.

Warriner, C.C., Lemmon, W.B. and Ray, T.S. (1963). Early experience as a variable in mate-selection. - Anim. Behav., 11, p.221-224.

Wells, P.V. (1958). Indigo buntings in lazuli bunting habitat in Southwestern Utah. - Auk, 75, p.223-224.

Wilkins, (1915). Cited by Guhl (1942).

Wood-Gush, D.G.M. (1965). The social organisation of domestic bird communities. - Symp. Zool. Soc. Lond., 14, p.219-231.

Wood-Gush, D.G.M. (1963). Comparative psychology and ethology.- Ann. Rev. Psychol., 14, p.175-200.

Wood-Gush, D.G.M. (1956). The agonistic and courtship behaviour of the Brown Leghorn cock. - Anim. Behav., 4, p.133-142.

Wood-Gush, D.G.M. (1955). The behaviour of the Domestic Chicken: a review of the literature. - Anim. Behav., 3, p.81-110.

Wood-Gush, D.G.M. (1954). The courtship of the Brown Leghorn cock. - Anim. Behav., 2, p.95-102.

Wright, S. (1940). Breeding structure of populations in relation to speciation. - Amer. Nat., 74, p.232-248.

Wright, S. (1938). Size of population and breeding structure in relation to evolution. - Science, 87, p.430-431.

Wright, S. (1935). Evolution in populations in approximate equilibrium. - J. Genet., 30, p.293.

Wright, S. (1932). The roles of mutation, inbreeding, cross-breeding and selection in evolution. - Proc. 6th Int. Congr. Genet., p.356-366.

Wright, S. (1921). Systems of mating. - Genetics, 6, p.111-178.

Wynne,-Edwards, V.C. (1962). Animal Dispersion in relation to social behaviour, Oliver and Boyd, Edinburgh and London.

Appendix

A little of the work reported here has already been published as a con-joint paper. It should be noted that the results, experiments and interpretations put forward in that paper were solely the work of this author; it was felt to be fitting to include Dr. D.G.M. Wood-Gush in that article, since the original conception and initiation of this study was due to him, and his invaluable and experienced advice helped greatly throughout the study.

Potential ethological isolating mechanisms and assortative mating in the Domestic Fowl, by Alan Lill and D.G.M. Wood-Gush

Wright (1938 and 1940) pointed out the importance of the concept of effective population size in evolution, and suggested that it often differed from the apparent size. It is determined by the number of fertile animals, the sex ratio and the mating system. Behaviour can exert a significant effect on the mating system through such phenomena as non-random mating, which upsets the Hardy-Weinberg equilibrium law and modifies the genetic constitution of subsequent generations. Sexual isolation can be important in speciation, both in the preservation of genetic distinctness of sympatric species by precluding or restricting inter-specific gene-flow, and probably also, much more rarely, in the initiation of new species or populations (Popham, 1947). Ethological isolation also precludes gene wastage which can occur through production of sterile, non-viable

or unadaptive hybrids.

In recent years, several studies of ethological isolating mechanisms have appeared in the literature, notably those concerned with Drosophila. Sexual isolation between geographic races and species of Drosophila has been demonstrated (see, for example, Mayr, 1946; Bastock, 1956; Manning, 1959). Haskins & Haskins (1950) and Liley (1962) have observed ethological isolation in poeciliid fishes and Hunsaker (1962) in the Sceloporus torquatus group of lizards. Blair (1942), Blair & Littlejohn (1960) and Littlejohn (1959), amongst others, have described the importance of mating call variability in sexual isolation in various anuran species.

But studies of behaviour factors that determine or could potentially determine reproductive isolation are still comparatively few. At the intra-specific level, non-random mating is one such factor, and although several cases have been reported in the domestic fowl, its evolutionary importance has been largely overlooked. We are aware of the dangers and limitations inherent in carrying out such studies in domestic species, and in particular of using the observed results as a basis for too general speculation about sexual isolation in wild avian species. Nevertheless, if the mechanism underlying sexual isolation is to be more fully understood, it is essential that controlled laboratory studies should be carried out. The domestic chicken is a useful species for such work, since so many morphologically different breeds and strains exist, and

the species is an established laboratory animal. The experimental techniques used in the present study have some resemblance to the breeding conditions pertaining in some related wild gallinaceous species, particularly to those with a 'lek-type' courtship, where the males and females may be strangers and polygamy is practised. Possibly also, "no-choice" conditions have some resemblance to the type of situation described by Sibley (1959), in which two sympatric species, reproductively isolated throughout most of their range, hybridise in one location where the ratio of the two species individuals is disproportionate. Under these conditions, animals appear to mate with what would normally be biologically inappropriate partners.

Assortative mating has been reported in the domestic fowl by Upp (1928), who claimed that males exhibited mating preferences, and by Philips (1919), and Wood-Gush (1954) who reported non-random mating due to preferences exercised by females. Fisher & Hale (1956) showed that New Hampshire cocks reared with own-breed hens preferred females of their own breed to others, and Silson (1963) has interpreted some observations of Parker (1961) as probably being attributable to preferential mating, though mechanical isolation may also have been involved.

The present work was designed to investigate more fully the sexual isolation and non-random mating phenomena in the domestic chicken and to establish the relative importance of any preference exhibited by males and females. Male courtship

variability has been studied in some detail in an attempt to elaborate or confirm the observations of Wood-Gush (loc. cit.) on the role of quantitative courtship variability in assortative mating in the fowl.

MATERIAL AND METHODS

General.

Material used in the work was derived from two true breeds, White Leghorn and Brown Leghorn, and from two Broiler strains (originating from a four way cross, White Leghorn x Cornish Game x Light Sussex x Rhode Island) selectively bred for increased body weight to shank length ratio. Birds of three selected Brown Leghorn lines available in this laboratory were also used.

All observations were carried out in completely enclosed, artificially lit pens, the birds being observed from without through a "uni-directional" observation window. To analyse female mating preferences, males were introduced singly for 15 minute periods into small flocks (9-12) of laying hens, unless otherwise stated. Observations were carried out in the late afternoon, from 15.00-18.00, since it has been shown (Upp, 1928; Skard, 1937; Parker, McKenzie & Kempster, 1940; Long & Godfrey, 1952) that sexual activity is highest during this period.

The criterion of female preference for males was taken to be a deep voluntary sexual (or solicitation) crouch. Crouches resulting from overt aggression by the male, from bodily

contact with the male and all non-sexual crouches (Foreman & Allee, 1959) were not included. The incidence of copulation was also noted and detailed figures of male courtship were kept. Certain male courtship patterns were timed with a stop-watch (e.g. "tidbitting"). To keep females on the pen floor during testing periods, the portable roosts were removed. The males were housed throughout the study, which extended over 14 months, in individual battery cages.

Male "preference" was studied in two ways. (1) In the Breeding Line (Brown Leghorn) males were introduced singly into a small group of females for short periods and mating behaviour patterns orientated towards specific labelled females noted. (2) The sexual "preferences" of males of three breeds for females of these breeds was studied in a "choice-situation". Males were released singly for short periods into an observation pen where they were confronted with a "choice" of two caged hens of different breed. Behaviour directed towards each female was noted and timed.

Strict controls were employed throughout the study where necessary, and partially randomised testing schedules precluded or minimised both male and female satiation. Analyses of variance, chi-square tests and correlation coefficients were the chief statistical tests used to evaluate the numerical data.

EXPERIMENT I: SEXUAL ISOLATION BETWEEN BREEDS AND STRAINS

Material and Methods.

The experiment was conducted on animals taken from two separate hatches. From Hatch 1 three flocks, one Brown Leghorn, one White Leghorn and one Broiler, each comprised of ten hens, were housed in separate observation pens. Of these, the Broiler and White Leghorn hens may have had visual experience of other breeds during the juvenile phase, the Brown Leghorn females had experience only of other Brown Leghorn stock. Seventeen males, six Brown Leghorn, six Broiler and five White Leghorn, were tested singly for two fifteen minute periods in each female pen.

From Hatch 2, three heterosexual flocks, one of each breed, of similar size were reared under conditions of visual isolation from all other breeds from hatching. A high mortality rate reduced the numbers of females to five White Leghorn, seven Brown Leghorn and eight Broiler by the time testing took place at 6½ months from hatching. Males had been removed from these flocks when the majority of females in each flock were in lay. Each female group was tested with six cocks of its own breed with which it had been reared, and six cocks of each of the other two breeds. Each male was tested twice with Brown Leghorn and Broiler hens and three times with the inbred White Leghorn hens whose sexual activity is low. Broilers used in these tests were from a different strain from those taken from Hatch 1, although from the same original foundation stock.

Results.

Hatch 1.

Brown Leghorn females solicited own-breed males significantly more than either White Leghorn or Broiler males ($p < .05$), (Fig.1), but did not discriminate between the latter two groups ($p > .05$). Neither White Leghorn nor Broiler females solicited the three male groups at significantly different rates ($p > .05$).

The copulation frequency between Brown Leghorn males and females was significantly higher than that between Brown Leghorn females and either Broiler or White Leghorn males ($p < .05$). No significant differences in copulation frequency between White Leghorn and Broiler hens and the three male groups were observed (Fig. 2). Neither was there any significant overall correlation between the degree of solicitation of male groups and the incidence of copulation with them. A significant potential unilateral sexual isolation was thus observed with respect to the Brown Leghorn breed, outgoing gene-flow to the Broiler stock being possible, but there existed a potentially effective block to incoming gene-flow from White Leghorn and Broiler stock.

An analysis of quantitative variance in male courtship and its relation to the observed sexual isolation phenomenon was made. The courtship of all the male groups to Brown Leghorn females, the only females which discriminated between males and exhibited mating preferences, is summarised in Table 1.

Fig. I. Solicitation of the three male breed groups by females of the first Hatch

Fig. 2. Copulation incidence in tests between males and females from the first Hatch

TABLE I

Courtship of Brown Leghorn hens by three male breed groups
(from Hatch I)

Male group	Total displays	Waltz	Wing flap	Tidbit	Feather ruffle	Head shake	Self-preen	Tail wag	Bill wipe	Cornering	Calls	High step	Rear approach	Strut
Brown Leghorn	919	162	82	282	25	145	31	1	16	3	139	11	19	2
White Leghorn	948	227	108	182	61	141	31	0	6	0	219	37	4	-1)
Broiler	1097	130	125	272	25	65	2	0	2	-1)	398	8	2	-1)

1) This display has never been observed in present material of this breed or strain.

No significant correlations between total display activity, total duration of "tidbitting", or total numbers of any specific display by males in thirty-four tests involving Brown Leghorn hens was observed. Some quantitative variance in certain aspects of the male groups courtship to these females did occur, but was not correlated with the observed female solicitation preferences. A significant overall variance in the amount of sexual vocalisation (calls) was noted ($p < .01$), Brown Leghorn cocks "calling" less than the other male groups, but any possible functional significance of this finding remains obscure.

Clearly quantitative variance in male courtship display alone did not account for the observed mating preferences of Brown Leghorn females. It would appear that these females discriminated between the male groups on other, as yet unknown, factors.

Hatch 2:

Brown Leghorn hens exhibited similar own-breed preferences to those of Hatch 1 females, soliciting own-breed cocks significantly more than either of the other two groups ($p < .05$). They did not discriminate between Broiler and White Leghorn males ($p > .05$). Broiler hens similarly solicited Brown Leghorn cocks more than any others ($p < .05$), but failed to discriminate between the other two male groups. White Leghorn hens exhibited a significant preference for own-breed cocks ($p < .05$), but did not discriminate between the Broiler and

Brown Leghorn males (Fig. 3).

No significant differences in the copulation rates between the male groups and the different female groups was observed ($p > .05$). (Fig. 4). This was attributable to the inefficient copulatory technique of these younger males, which were less sexually experienced with receptive hens than those of Hatch 1. Thus no significant correlation between the observed female mating preferences and the coition incidence was apparent, but Brown Leghorn cocks had more incomplete matings with own-breed than with White Leghorn or Broiler females.

Quantitative aspects of male courtship display of Hatch 2 birds are given in Table 2. It was apparent from the observations made that the three female breed groups discriminated between the different males on visual cues other than quantitative variability in courtship. Brown Leghorn and Broiler females responded extremely aggressively to Broiler and White Leghorn cocks immediately on their entry into the test-pen and prior to displaying. The Broiler males established dominance over both female groups, but were subsequently avoided by the hens, whilst the White Leghorn males rarely established dominance over the two groups of females and fled from them; in several instances they had to be prematurely removed from the Broiler females to avoid their being severely wounded. White Leghorn hens similarly discriminated between males immediately upon their entry into the test-pen, fleeing rapidly from all except own-breed males, which they immediately approached. They

Fig. 3. Solicitation of the three male breed groups by Hatch 2 females.

Fig. 4. Copulation incidence in tests between males and females from Hatch 2.

TABLE 2

Courtship of females of the three 'breeds' by males of each breed (from Hatch 2)

Male group	Total displays	Waltz	Wing flap	Tidbit	Feather ruffle	Head shake	Self-preen	Tail wag	Bill wipe	Cornering	Calls	High step	Rear approach	Strutting	
Brown Leghorn	1143	255	154	236	15	100	5	4	11	27[2]	374	-	6	5	To
White Leghorn	184	14	15	32	10	36	5	-	4	-	68	-	-	-[1]	Brown Leghorn
Broiler Strain	1175	113	226	232	27	85	8	-	-	-[1]	502	-	-	-[1]	♀♀
Brown Leghorn	549	27	91	172	20	195	10	6	34	-	37	3	-	8	To
White Leghorn	1623	296	113	583	73	110	12	1	21	1	561	2	-	-[1]	White Leghorn
Broiler Strain	1292	81	403	367	38	114	22	-	-	-[1]	266	2	-	-[1]	♀♀
Brown Leghorn	956	270	82	208	9	96	16	6	15	16	229	4	-	5	To
White Leghorn	49	4	-	1	1	3	4	-	-	-	36	-	-	-[1]	Broiler ♀♀
Broiler Strain	1287	144	174	314	21	81	8	-	-	-[1]	605	1	-	-[1]	

1) These displays have never been observed in present material of these strains.

2) Performed mostly by one male.

continued to avoid Brown Leghorn males exhibited a high latency to approach and court own-breed hens, but generally did so after several minutes had elapsed. The above observations were indicative of a female discrimination between males based, at least partially, on physical characteristics.

Some quantitative variance in display performances to the female groups by the three male groups was observed (see Table 2), but it was almost entirely attributable to the different manner in which females responded to them. The "cornering" display is more typical of younger males, and has an observable stimulatory effect on the female, which approaches the displaying male rapidly. It has never been observed in the present Broiler stock and occurs only rarely, and in an attenuated form, in the White Leghorn stock used. Brown Leghorn cocks "cornered" significantly more to Broiler hens than did the other males. However, there was no significant variance in the amount of "cornering" the different male groups performed with the other groups of females of Hatch 2, or with the groups of females of Hatch 1. Therefore it seems unlikely that quantitative breed differences in the performance of this display are important in the female discrimination.

White Leghorn cocks "waltzed" significantly more than other males to White Leghorn hens ($p < .01$), and were solicited more by them. Broiler and Brown Leghorn cocks were not solicited differentially by these females, and did not differ significantly in their "waltzing" to them. Evidence is presented later to

show that waltzing may exert an effect on females solicitation preferences. It is, however, entirely possible that the low rate of waltzing of Brown Leghorn and Broiler males to White Leghorn females occurred because the females avoided them markedly.

Quantitative variance in male courtship display alone did not account for the observed female discriminations and preferences in either hatch. The discrimination appeared to be based primarily on some other, probably physical, differences between males.

Brown and White Leghorn females of both hatches showed essentially similar own-breed mating preferences. Hatch 1 White Leghorn hens were older females than those from Hatch 2 and were sexually unreceptive, but more extended tests with them, yielding more data, may well have revealed a truly significant preference for own-breed cocks.

Females of the two Broiler strains differed significantly in their mating preferences, however, but it is not yet clear whether this reflects a true strain difference since Hatch 1 females were older than those of Hatch 2 and their early experience was not fully known. The preference of the Alpha strain Broiler hens of Hatch 2 for Brown Leghorn males is of especial interest, and cannot be regarded as an innate preference for "brown-ness" itself, since these hens did not prefer the brown individuals amongst the Broiler cocks to others. The significance of this finding is discussed more fully later.

EXPERIMENT II:

SEXUAL ISOLATION BETWEEN BROWN LEGHORN LINES

Material and Methods.

Two flocks each of 9 Breeding Line Brown Leghorn hens were kept in separate observation pens. Four males of each of three Brown Leghorn lines, Breeding, Red and White, were tested singly for two fifteen-minute periods in each pen, i.e. in a "no-choice" situation. The males of these lines differ markedly in plumage colour, size, conformation, vocalisation, etc. Breeding line males have a black ventral aspect, whilst the dorsal feather tracts each have a specific hue, ranging from amber to chestnut brown. Red line males are shorter, smaller, and the plumage is an un-patterned chestnut colour throughout. Their vocalisations are of a higher pitch than Breeding line Males. White line males, though similar in size to Breeding line males, have a plumage showing some patterning, but with a white mottled effect. Their vocalisations differ in pitch etc. from both the other lines.

The hens had no previous sexual experience of Red or White line males, but had experience of Breeding line males. One Red line male and one White line male were excluded for two and one tests respectively as they were unwell.

Results.

There was a significant variance in female solicitation of the three groups of males ($p < .05$). Breeding line hens solicited Breeding line cocks significantly more than either

Red or White line cocks ($p < .05$), but did not distinguish significantly between Red and White line cocks ($p > .05$) (Fig. 5).

There was also a significant variance in copulation frequency between Breeding Line hens and males of the three lines ($p < .05$) (Fig. 6). There was a significantly greater copulation frequency between Breeding line hens and cocks than between Breeding line hens and Red and White line cocks ($p < .05$), but no significant difference in copulation frequency between Breeding line hens and Red males and Breeding line hens and White males was observed ($p > .05$). There was a significant correlation between differential female solicitation and copulation incidence ($p < .05$).

Breeding line hens thus exhibited own-line preferences and there was effective sexual isolation between them and Red and White line males. Both female groups had similar preferences and individual and group female preferences were closely correlated. Some Breeding line males elicited significantly more female solicitation than others ($p < .05$).

An analysis of quantitative variance in display between the male groups was made, and the relationship between such variance and differential female solicitation was studied. Some variance in "tidbitting" occurred. In this display, described as a "displacement reaction" by Wood-Gush (1956), the male pecks at the litter, feathers etc., scrapes with his feet and gives a high-pitched, segmented call. A significant negative correlation between the mean tidbitting duration and female

Fig. 5. Breeding Line females' solicitation of males of three Brown Leghorn lines.

Fig. 6. Copulation incidence between Breeding Line hens and cocks of three Brown Leghorn lines. Asterisks show complete absence of copulation.

crouching was observed ($p < .05$). White and Red strain males spent significantly longer tidbitting than Breeding strain cocks ($p < .05$), but did not differ significantly from each other in this respect. Most of this tidbitting was of low intensity. This display type is thought to be indicative of low sex "drive" in the male. Breeding line males showed a significantly higher mean display rate than White line males ($p < .01$), but did not differ significantly from the Red line. No correlation between mean number of displays performed and female solicitation was observed, however. The Breeding line cocks 'called' more than White line males ($p < .05$), but did not differ significantly from Red males. Display performance is summarised in Table 3.

The comparatively small degree of quantitative variance in display between the three male groups was not significantly correlated with the observed female solicitation preferences. If male display variance exerted an effect on female preferences, the effect would appear to be too complicated to be detected by the relatively simple measures taken in this work. That the females discriminated between males on non-behavioural characteristics was indicated by the observation that they sometimes crouched to Breeding line males as they entered the pen, prior to displaying, but were never observed to respond in like manner to Red or White males.

TABLE 3

The mean rate and form of courtship display in males of the three Brown Leghorn lines

Line	Waltz	Wing flap	Tidbit	Feather ruffle	Head shake	Preening	Tail wag	Bill wipe	Corner-ing	Rear approach	High step	Strut	Calls	Mean displays
Breeding	12	11	14	1	6	0	0	1	1	4	2	0	22	82
Red	3	32	14	1	4	0	0	0	0	0	1	0	8	57
White	3	1	26	1	4	0	1	0	0	0	1	0	0	44

EXPERIMENT III

ASSORTATIVE MATING WITHIN THE BROWN LEGHORN BREEDING LINE

Material and Methods.

Two flocks, each of 9 Breeding Line hens, were kept in separate observation pens and 6 Breeding Line cocks were tested for two 15-minute periods singly with each flock. All birds had previous sexual experience, one female had to be excluded at an early stage in the experiment due to sickness.

Results.

A significant difference between the solicitation frequency of the hens to the six males was observed ($p < .01$) (Fig.7). A significant difference ($p < .01$) also occurred in the copulation frequency between the Breeding Line hens and the six males (Fig.8). There was, however, no significant correlation between female solicitation and copulation incidence ($p > .05$).

The females of both flocks had significantly similar preferences, responding to the males in a similar manner. The preferences of the individual females were also like those of the flock as a whole. Variability in male courtship and its relationship to the assortative mating phenomenon were analysed (Table 4). Some degree of variability between the males in certain aspects of courtship occurred (cornering and tidbitting), but there was no significant correlation between such variability and the differential success of the males in evoking female solicitation.

Fig. 7. Solicitation frequency of Breeding Line females to six Breeding Line cocks.

Fig. 8. Incidence of copulation between Breeding Line hens and cocks. Asterisks indicate zero readings.

TABLE 4

The rate and form of courtship display of the six Breeding Line cocks

Male	Waltz	Wing flap	Tidbit	Feather ruffle	Head shake	Preen-ing	Tail wag	Bill wipe	Corner-ing	Rear approach	High step	Strut	Calls	Mean displays
3653	39	61	49	12	20	1	0	10	20	0	3	1	103	319
3649	54	41	55	14	31	0	0	2	5	19	8	0	38	269
195	63	60	69	12	30	1	0	0	0	27	13	0	66	344
194	42	29	53	7	18	2	0	17	0	11	27	0	89	296
3878	40	30	58	16	72	0	0	0	4	39	19	0	70	359
3672	23	40	136	5	42	6	0	5	0	0	0	0	18	276

Although there was no significant correlation between variance in male "Waltz" and "Rear Approach" rates and female solicitation, a sequential analysis of the male courtship displays showed these two displays to be important in eliciting female solicitations. Of the ninety-nine crouches which occurred in this experiment, sixty-three were preceded by some male display. An analysis of the series of displays occurring shortly before crouching was made. Such series never contained more than three displays occurring before crouching, but sometimes contained only a single display if, for example, a crouch had occurred almost immediately after the male's entry into the test pen. This analysis revealed that only five of the known repertoire of thirteen courtship displays occurred significantly in such series. Their occurrence is listed in Table 5. Further, an analysis of the single display preceding each crouch showed that only the Waltz and Rear Approach occupied thisposition to any significant degree (p in both instances $< .05$ in a chi^2 test of significance). These two displays elicited 72.5 per cent of all female solicitations in this experiment. The relationship of these two displays to female solicitation was not linear, and a more subtle relationship may exist. Despite this lack of an overall linear relationship, it is of interest to observe that the two males which elicited least female crouching failed to perform the Rear Approach and differed significantly from all other cocks in this respect.

TABLE 5

Occurance of male displays shortly before female crouching from a sequential analysis. (For the extent of the sequences see the text)

Display	Percentage occurrence in sequences	Significance of Occurrence
Rear Approach	57.5	
Wing flap	43.9	Significantly greater occurance than expected ($p < .01$)
Calls	36.4	
Waltz	30.3	
Tidbit (high intensity)	28.8	
Headshake	16.6	Not significantly greater than expected
Tidbit (low intensity)	7.3	Significantly lower occurrence than expected ($p < .05$)
Feather ruffle	6.1	
Bill wipe	3.0	
Strutting	1.5	
High Stepping	1.5	Significantly lower occurrence than expected ($p < .01$)
Cornering	1.5	
Tail wag	0.0	
Self-preening	0.0	

It is tentatively suggested that "Wing-flapping" , "high-intensity tidbitting", and "Calling", the other displays which occur to a significant degree in sequences of displays preceding solicitation, raise the level of sexual "excitement" or arousal in the female. All have a marked sound component. It is interesting to observe that of the two males which elicited least female solicitation, one (3672) did significantly more low intensity "tidbitting" than any other male ($p < .01$), and the other (3653) "cornered" significantly more than any other male ($p < .01$). Wood-Gush (1956) has described these activities as resulting from either a conflict between flight, aggression and sex tendencies, or thwarting of the sexual tendency. Low intensity tidbitting is typical of a male which is not highly sexually motivated, the 'flight component' seems to be dominant in this form of the display.

EXPERIMENT IV

MALE MATING PREFERENCES IN THE BROWN LEGHORN BREEDING LINE

The lack of a significant correlation between female solicitation and coition incidence in infra-line tests of the Breeding Line (Experiment III) might possibly be due to male preferences for certain females. The net genetic effect of a non-random mating system can only be determined by analysing both male and female preferences, if both are involved in determining the incidence of coition.

Material and Methods.

Eight Breeding Line cocks were tested singly for four fifteen minute periods each in an observation pen containing eight marked Breeding Line females. (Since identification of each individual hen was necessary, it was not thought practicable to increase this figure). Observations extended over sixteen days. Crouching of females was noted and also male mating activities which were orientated to a specific female. These activities were mounting, treading and copulating after a female had crouched; attempted mounting of a female (grabbing and chasing, placing a foot on the hen's back); rape (complete copulation with an unreceptive hen) and forced interrupted mating (hereinafter abbreviated to F.I.M.; a case of rape which terminates before actual cloacal contact occurs). It was thus possible to analyse male preferences taking into account female preferences simultaneously. A time record was taken during each test so that any effects of satiation could be allowed for in the analysis.

Results.

The observed interactions are summarised in Tables 6 and 6a.

Female solicitation behaviour exerted a powerful effect on male mating behaviour, in that males only copulated with hens which crouched to them (only one case of complete rape occured).

TABLE 6

Crouching by eight Breeding Line hens in response to the courtship of eight Breeding Line cocks

Males	Crouches by female								Total for individual males
	542	349	566	346	559	568	348	541	
I	1	1	3	2	4	2	1	1	15
II	0	2	0	0	0	0	2	0	4
III	0	2	0	1	1	1	0	0	5
IV	0	5	0	3	1	2	1	0	12
V	1	1	3	0	4	0	2	2	13
VI	1	0	0	1	7	4	3	1	17
VII	2	2	3	2	3	2	1	1	16
VIII	1	0	0	1	7	4	3	1	17
Total crouching for individual females	6	13	9	10	27	15	13	6	99

TABLE 6a

Mating behaviour patterns of eight Breeding Line males orientated to specific individual hens

Males	Male mating activities	Females 542	349	566	346	559	568	348	541
I	Percentage female crouches evoking male response (to nearest whole figure)	100	0	66	50	50	100	0	100
	Copulations (completed)	---	---	1	1	1	2	---	---
	Att. M.) Male initiated	---	---	1	2	---	---	---	---
	Rape) mating activities	---	---	1	---	---	---	---	---
	F.I.M.)	---	---	---	---	---	---	1	---
II	Percentage, etc	---	0	---	---	---	---	0	---
	Copulations (completed)	---	---	---	---	---	---	---	---
	Att. M.) male initiated	---	---	---	---	---	---	---	---
	Rape) mating activities	---	---	---	---	---	---	---	---
	F.I.M.)	---	---	---	---	---	---	---	---
III	Percentage, etc	---	50	---	100	100	100	---	---
	Copulations (completed)	---	1	---	1	1	1	---	---
	Att. M.) male initiated	---	---	---	---	---	---	---	---
	Rape) mating activities	---	---	---	---	---	---	---	---
	F.I.M.)	---	---	---	---	---	---	---	---
IV	Percentage, etc	---	40	---	33	0	50	100	---
	Copulations (completed)	---	---	---	---	---	1	---	---
	Att. M.) male initiated	---	---	1	3	---	1	---	---
	Rape) mating activities	---	---	---	---	---	---	---	---
	F.I.M.)	---	---	---	---	---	---	---	---
V	Percentage, female crouches evoking male response (to nearest whole figure)	100	0	100	---	75	---	100	100
	Copulations (completed)	---	---	3	---	---	---	1	2
	Att. M.) male initiated	1	---	2	---	---	---	2	---
	Rape) mating activities	---	---	---	---	---	---	---	---
	F.I.M.)	---	---	---	---	---	---	---	---
VI	Percentage, etc	0	---	---	0	71	50	33	0
	Copulations (completed)	---	---	---	---	3	2	---	---
	Att. M.) male initiated	---	---	---	---	1	1	1	---
	Rape) mating activities	---	---	---	---	---	---	---	---
	F.I.M.)	---	---	1	---	---	1	---	1
VII	Percentage, etc.	50	100	100	100	66	50	0	100
	Copulations (completed)	1	1	1	1	---	---	---	1
	Att. M.) male initiated	---	2	---	---	1	---	---	1
	Rape) mating activities	---	---	---	---	---	---	---	---
	F.I.M.)	1	1	1	---	---	---	---	---
VIII	Percentage, etc.	0	---	---	0	71	50	33	0
	Copulations (completed)	---	---	---	---	3	2	---	---
	Att. M.) male initiated	---	---	---	---	1	1	1	---
	Rape) mating activities	---	---	---	---	---	---	---	---
	F.I.M.)	---	---	1	---	---	1	---	1

Female receptivity and passivity thus seemed to be necessary if copulation was to take place, the struggling of an unreceptive female preventing cloacal contact or deterring the mating cock before coitus was achieved. Males did not, however, prefer those females which crouched more to them, since they did not copulate more with them, attempt to mount them more or have more forced interrupted matings with them than with other females (the correlation in all cases was non-significant, $p. > .05$).

Males only copulated with a mean of 39.5 per cent of the females which crouched to them. This could not be regarded as a preference for certain of the receptive hens, since neither the male group nor individual males copulated significantly more with some hens than others (p in both cases $> .05$). The percentage of crouching females copulated with was apparently due to satiation rather than preference. Males did not have significantly more attempted mountings on F.I.M.'s with some hens than others ($p > .05$).

Under present experimental conditions, male preference was not observed. It is felt that a longer study, yielding more data, particularly if involving males permanently resident with females, might reveal true male mating preferences. In the present work, males copulated with females in a fairly random manner, but where the sexes are mutually acquainted this may well not be so.

EXPERIMENT V:

MALE PREFERENCES FOR FEMALES OF DIFFERENT BREEDS IN A CHOICE-SITUATION

The lack of a significant positive correlation between differential solicitation of males by hens and the incidence of copulation in Experiment I may be attributable in part of male mating "preferences". However, comparatively little significant quantitative difference was observed in the courtship of hens of different breeds by specific males under the "no-choice" conditions of this experiment. If male "preference" is important in sexual isolation between the breeds under these conditions, it must be exerted during copulatory activities rather than in courtship itself.

In wild species, male preferences which parallel those of females could greatly strengthen sexual isolation. It was therefore thought desirable to determine whether males showed sexual "preferences" under true choice (as opposed to "no-choice") conditions. Ideally, such "preferences" could be tested by releasing males singly into flocks consisting of equal numbers of hens of different breeds (i.e. multiple-choice). If such a technique was used, however, one found that in the domestic fowl it was extremely difficult to analyse male "preference" due to the differential responsiveness of females. Thus a procedure was employed which precluded this latter effect.

Males were released singly into an observation pen (Fig.9) in which they were confronted with a "choice" of two females, each of a different breed. These females were in two separate, cylindrical, wire-mesh cages, equidistantly placed

Fig. 9. I. Plan view of test pen used to determine male preference in a choice-situation. II. A cage in which the cue female was placed in the choice-situation. Measurements in inches.

from an entrance tunnel through which the male was admitted. The pen floor was swept fairly free from litter etc. throughout the experiment, and was divided into three areas, A, B and C, by white lines. Areas A and B surrounding the cages were designated cage areas, and were of equal size, Area C was a neutral zone.

Males were released into the test pen for ten minute periods and their behaviour observed. The time spent in each cage area and the total number of displays in each cage area were noted. The number of "waltz" displays to each caged hen was also recorded. Of these three measures, the last is probably the best gauge of male preference, since only the "waltz" and "rear approach" displays of the domestic cock are oriented to a specific female. The "rear approach" does not occur under present conditions, but "waltzing" was frequent (Figure 10).

Each male was tested twice in three separate discriminations, namely, Brown Leghorn/Broiler, Brown Leghorn/White Leghorn and Broiler/White Leghorn. In the second tests the position of the females was reversed to ensure that male "choice" was a choice of females and not just a tendency to favour, for example, Area B to Area A. Half the males of each breed were tested with one group of three females (Group I females): the other half were tested with a second group of three females (Group II females) to detect whether any male preferences shown were for particular breeds and not for particular individual

Fig. 10. A Brown Leghorn cock avoids the cue White Leghorn in Cage Area A, and "waltzes" to the caged Brown Leghorn hen in Area B.

hens. A period of seven days was allowed to elapse between consecutive tests of any male to avoid males becoming too familiar with the experimental situation. Initial choice of a caged female immediately after the cock's entry did not prove to be a useful preference criterion, since many cocks entered the pen far too rapidly.

Six Brown Leghorns, six Alpha strain Broiler and six White Leghorn males, which had been reared with their own breed or strain females, were used. Of these, the Broiler and White Leghorn cocks had had a little sexual experience of the other breeds since maturation, the Brown Leghorns had none. In addition, five Brown Leghorn, two White Leghorn and four Broiler males which had been raised in a "tri-breed" heterosexual flock were also tested to determine whether juvenile experience of the other breeds affected male preference. All birds, except the Brown Leghorn males of only homogamic experience, had been used in Part 2 of Experiment I.

Results.

Tables 7 and 8 summarise the observed preferences of the males. Preference was deemed to have occurred only when results for males tested with Group I females and males tested with Group II females and the combined results were the same for any one measure taken. A solid circle in Table 8 thus represents a preference in one measure exhibited by males tested with both female groups and in the two sets of data combined. An open circle indicates that preference occurred in a particular measure in all three sets of data, but that one

TABLE 7

Male sexual activity directed to females of different breeds in a "choice-situation"

ales	Early experience		Discriminations					
			Broiler	Br.Leghorn	Wh. Leghorn	Br. Leghorn	Broiler	Wh. Leghorn
		Waltz	63	100	1	132	165	1
Brown		Total Display	214	380	73	454	450	37
Leghorn	Homogamic	Secs. in Cage Area	1575	3447	922	4571	4536	571
		Waltz	23	16	15	11	25	12
Brown	Homo +	Total Display	172	248	121	170	179	159
Leghorn	Heterogamic	Secs. in Cage Area	2615	1734	1927	2818	2558	2422
		Waltz	11	1	30	2	22	20
White		Total Display	104	85	325	36	147	261
Leghorn	Homogamic	Secs. in Cage Area	1317	1581	4297	376	1247	3526
		Waltz	22	6	8	7	24	0
White	Homo +	Total Display	87	56	88	35	106	25
Leghorn	Heterogamic	Secs. in Cage Area	992	832	1211	562	1187	479
		Waltz	63	43	20	65	101	26
Broiler		Total Display	284	184	98	323	450	127
strain	Homogamic	Secs in Cage Area	3131	1895	1195	3830	4792	1162
		Waltz	20	21	5	41	67	5
Broiler	Homo +	Total Display	109	207	103	231	219	128
strain	Heterogamic	Secs. in Cage Area	905	2147	832	1937	1674	1708

TABLE 8

Male discrimination and "preferences" for females of three "breeds" (Summary of data in Table 7), Legend in text

Males	Early experience	Broiler: Br. Leghorn	Wh. Leghorn: Br. Leghorn	Broiler: Wh. Leghorn
Brown Leghorn	Homogamic	Preferred ● Br. Leghorn ○	Preferred ● Brown Leghorn ● ●	Preferred ● Broiler ● ●
Brown Leghorn	Homo + Heterogamic	Preferred ● Brown Leghorn	No preference	No preference
White Leghorn	Homogamic	No preference	Preferred ● White Leghorn ○	Preferred ● White Leghorn ●
White Leghorn	Homo + Heterogamic	No preference	Preferred ● White Leghorn	Preferred ● Broiler ● ●
Broiler	Homogamic	No preference	Preferred ● Brown Leghorn ●	Preferred ● Broiler ● ●
Broiler	Homo + Heterogamic	Preferred ● Brown Leghorn	No preference	Preferred Broiler ○

of the readings was significant only at a 5% level as opposed to a 1% level.

Brown Leghorn males of mixed (homo and heterogamic) early experience were less sexually active than those of solely homogamic experience, displaying less frequently and at lower intensities. Most birds performed adequately in the test-situation, though the White Leghorn cocks showed a greater latency in approaching the cage areas than other males. No tendency to prefer cage area A to area B was observed.

Some differences in the discrimination between the cue females were observed between males tested with Group I hens and those with Group II hens. They were, however, not consistent and it is doubtful if they were attributable to differences in stimulative value between the two cue females of any breed. Breed preferences rather than preference for an individual cue female seemed to occur.

The observed male preferences can be summarised as follows:

(1) Brown Leghorn and White Leghorn cocks of homogamic early experience exhibited marked significant preferences for homogamic females.

(2) Broiler strain cocks of similar early experience showed a preference for homogamic hens in only one of the two discriminations in which such females were involved.

(3) Brown Leghorn and Broiler strain males of homogamic experience preferred Broiler and Brown Leghorn hens respectively to White Leghorns in tests where females of their own strain were not involved. Both preferred the darker coloured strain

under these conditions.

(4) White Leghorn cocks of similar experience showed no preference in the test not involving White Leghorn females and the less marked contrast in colour between the cue Brown Leghorn and Broiler females may have been important in this respect.

(5) Brown and White Leghorn males of mixed early experience differed in their discrimination from their counterparts of solely homogamic experience. Both exhibited only a weak preference for homogamic hens in only one of the two tests in which they were presented with them.

(6) Broiler cocks of mixed experience, like their counterparts of homogamic early experience, preferred homogamic hens in only one of two tests in which they encountered them, but this preference was significantly weaker than that of homogamic experienced Broiler cocks.

(7) None of the three groups of males of mixed experience showed any significant preference in tests involving solely heterogamic females.

Two other important differences in the responses of the males of mixed experience were observed. The two White Leghorn males strongly preferred Broiler to White Leghorn hens and the Broiler males showed a weak preference for Brown Leghorn as opposed to Broiler hens. The first finding is of especial interest, since these two males, unlike their counterparts of 'own-breed' juvenile experience, strongly

resisted the violent and aggressive discrimination against them by Broiler hens when given the type of open-pen sexual isolation tests described for Hatch 2 of Experiment I, and succeeded in occasionally courting them.

This seems to suggest that dominance relationships in the juvenile phase may be of importance in facilitating any learning process involved in preferential mating. Broiler cocks of mixed early experience also differ somewhat in their preferences from those with solely 'own-strain' experience, but these differences remain difficult to interpret as yet.

Under 'choice' conditions, therefore, males of homogamic early experience showed some statistically significant preferences for homogamic females. Males of mixed early experience showed only slight homogamic preferences and in one case, that of the White Leghorns, dominance relationships in the juvenile phase seem to have been important in establishing a preference for heterogamic females.

DISCUSSION AND CONCLUSIONS

Potential ethological isolating mechanisms have been observed between breeds and strains of the domestic fowl. The isolation phenomenon was most strongly developed in the Brown Leghorn Breeding Line, which bears close phenotypic similarities to the ancestral Red Jungle fowl (Gallus gallus spadiceus) and may therefore be considered as being close to the 'wild-type' chicken.

Females exhibit preference for some males by soliciting

them in a deep, sexual crouch more than others which they avoid and/or exhibit overt aggression towards. Brown and White Leghorn females show preferences for own-breed (homogamic) or own-strain males, a tendency which, in wild species, could well augment other mechanisms precluding out-breeding. The lack of an overall correlation between preferences of females and the observed incidence of coition was not attributable to male mating preferences, since males differed little in their courtship of females of different breeds under "no-choice" situations. Nor can quantitative differences in male courtship display be of much importance in breed and strain "recognition" by hens, an integral process in sexual isolation. Males of different breeds and strains showed few quantitative differences in courtship display, and such differences as did occur were not correlated with the solicitation preferences shown by the females. Other factors, such as differences in plumage colour, vocalisation, morphology, etc. seem likely to be involved in discrimination of males by females. A tendency of 'unsuccessful' males to exhibit a higher frequency and duration of displays described by Wood-Gush (1956) as the outcome of an internal conflict between the attacking, fleeing and sexual tendencies, or of a thwarted sex drive, was observed. Which is cause and which effect under these conditions is not known.

In wild species, sexual isolation could be enhanced if males exhibit homogamy as well as females. In a choice

situation which effectively precluded stimulation of males by female sexual responses, males which had been reared with own-breed hens courted own-breed hens more than others. The results and testing technique indicated that true breed "recognition" and preference rather than preference for individual females was involved. Since female sexual responses were precluded and the stimulus hens did not call to any significant degree, purely visual cues appear to play an important role in breed "recognition" by males. This was substantiated by two further observations. Own-breed preference was enhanced when the own-breed and the other cue females were of markedly contrasting plumage hue, and in tests involving a 'choice' of two heterogamic (other-breed) hens, discrimination between them was enhanced when a similar disparity in plumage colour occurred. Plumage colour thus appears to be involved in the male breed "recognition" process, and it seems possible also that own-breed "recognition" is enhanced by reference to another breed. This finding may partially explain the apparent lack of discrimination under "no-choice" conditions. The results are in agreement with those of Fisher & Hale (loc. cit.), in that White Leghorn females elicited least sexual behaviour in all but own-breed cocks.

The preference of Alpha strain Broiler hens for Breeding Line males is of special interest. These hens were hatched and reared with own-strain cocks, but responded at maturity very aggressively to them and to White Leghorn cocks. Taylor

& Sluckin (1964) have demonstrated that domestic chicks hatched and reared communally appear to imprint to their siblings. Whether imprinting to siblings occurs in nature, or whether it is simply the result of the absence of the normal imprinting object, the mother, does not appear to be known. Clearly it could have some adaptive value in initiating flocking, which could afford protection to the chicks. It would appear, however, from the observed mating preferences of adult Alpha Strain Broiler hens, that imprinting to siblings does not directly affect adult sexual preferences in the way that imprinting to the mother may, and this is perhaps not surprising in view of the extensive changes in colour and morphological characteristics which take place during juvenile development. This might point to an innate preference in the Alpha strain female for the Breeding Line, which could be considered as a preference for "wild-type", with all the attendant evolutionary significance. However, it is also possible that imprinting to siblings is a rather different, weakened or non-existent process in this line in which there is such individual variation in plumage colour, comb-shape etc. even from hatching. In view of the marked effect that juvenile learning (at a post-imprinting stage) had on the mating preferences of White Leghorn and Alpha Broiler cocks reared in a tri-breed flock, it is surprising that rearing with own-line males did not result in homogamic tendencies in Alpha females. The possibility of a truly innate preference for 'wild-type' clearly cannot be entirely

disregarded at this stage.

The observations of Wood-Gush (1954) on female mating preferences at an infra-line level were substantiated. In short (15 minute) tests no preference for individual hens exerted by males was observed. Copulation incidence was determined by female solicitation preferences and differential male copulatory activity, so that a significant correlation between female preferences and copulation incidence only occurred when a "preferred" male was also one of high sexual vigour. Cocks copulated with the individual hens in a fairly random manner. However, when male and females are mutually acquainted, as when a male is permanently resident in a pen, the male may then exhibit mating preferences. Upp (1928) carried out such a study and claimed that males showed preferences, but his data lack details of female solicitation and it is not thus possible to determine whether such preference occurred. Philips (1919) using shorter testing periods claimed that the hen's role was more important than the cock's in non-random mating.

A sequential analysis of male courtship display in the Breeding Line showed a relatio ship between the waltz and the rear approach and female solicitation. These two displays were the only ones preceding crouching to a significant degree. No linear overall correlation between numbers of these displays performed and degree of female crouching occurred. However, the two males which elicited least female crouching (3653 and

3672) did not rear approach and differed significantly from all other males in this respect. 3653 cornered significantly more than other males and this display stimulates the females to approach the male, and may increase sexual arousal in the hen. 3672 tidbitted at a low intensity more than other cocks; this form of the display appears to be indicative of low sexual motivation and may contain a strong element of "fear". These findings are similar to those of Wood-Gush (1954) who found a similar lack of an overall exact correlation between quantitative male courtship variance and female sexual preferences, but correlation in some aspects, and of an incomplete nature.

Some evidence exists (Lill, unpublished data) that the relationship between waltzing and crouching may involve a "threshold" type of effect, whereby females become receptive only after the amount of waltzing has exceeded a specific level. It was also observed that tidbitting (high intensity), wing-flapping and sexual vocalisation occur significantly shortly before crouching. These displays are interpreted as stimulating sexual arousal in the hen; all have a marked sound component. Thus a waltz display preceded by one of these 'arousal' displays may be more efficacious in stimulating female crouching than one which is not. A subtle relationship between waltzing and crouching rather than a linear one seems to be implied, and further sequential analysis is to be undertaken.

Females, however, discriminate between own-strain cocks

on other factors also. Some males received crouches on entering a pen, prior to displaying, others did not. Visual cues based on small, subtle, morphological differences may be important in this respect. Behavioural variability alone does not account for the assortative mating phenomenon. Early experience of other breeds, excluding the possibility of imprinting on them, in the classical sense, weakened male own-breed preferences significantly compared with controls. It resulted in some preferences for heterogamics also. If an innate tendency to mate with own-breed hens exists, or if imprinting to siblings occurs, clearly neither exerts an unmodifiable effect on subsequent adult sexual preferences. Early learning can exert an effect on mating preferences of the domestic cock in at least some instances. Further work on this problem is in progress.

SUMMARY

(1) Potential ethological isolating mechanisms were observed between breeds and strains of domestic fowl.

(2) Brown and White Leghorn females exhibited homogamy, but females of a Broiler strain showed a preference for Breeding Line Brown Leghorn males, which bear a close phenotypic resemblance to the Red Jungle fowl (Gallus gallus spadiceus).

(3) Observations indicated that females discriminated between males on physical characteristics rather than quantitative differences in male courtship.

(4) In a "choice-situation", males which had been reared with own-breed females courted caged own-breed hens significantly more than others. Males reared with their own and other breeds showed only weak own-breed preferences, and in two cases, heterogamy was observed.

(5) Males apparently discriminated between females on visual cues, particularly female plumage colour.

(6) Assortative mating within a single line was also observed, females preferring some males to others. Quantitative differences in male courtship were not important in this respect.

(7) In tests of short duration, males did not exert preferences for individual hens of a single line.

(8) A sequential analysis of the courtship of the Brown Leghorn cock revealed that two displays were important in

evoking female solicitation, namely the waltz and the rear approach. Three other displays were interpreted as increasing sexual arousal in the female.

(9) The evolutionary significance of some of the results is briefly discussed.

"From Behaviour, 25, p.16 (1965)".

(Figures are not reproduced here since they are included in the main text of the thesis).

REFERENCES

Bastock, M. (1956). A gene mutation which changes a behaviour pattern. - Evolution 10, p.421-439.

Blair, A.P. (1942). Isolating Mechanisms in a complex of four species of toads. - Biol. Symp. 6, p.235-249.

Blair, W.F. & Littlejohn, M.J. (1960). Stage of speciation of two allopatric populations of chorus frogs (Pseudacris).- Evolution 14, p.82-87.

Fisher, A.E. & Hale, E.B. (1956). Stimulus determinants of sexual and aggressive behaviour in male Domestic Fowl.- Behaviour 10, p.309-323.

Foreman, D. & Allee, W.C. (1959). A correlation between positive posture stance and outcome in paired contests of domestic hens. - Anim. Behav. 7, p.180-188.

Haskins, C.P. & Haskins, E.F. (1950). Factors governing sexual selection as an isolating mechanism in the Poeciliid fish Lebistes reticulatus. - Proc. Nat. Acad. Sci. 36, p.464-476.

Hunsaker, D. (1962). Ethological isolating mechanisms in the Sceloporus torquatus-group of lizards. - Evolution 16, p.62-74.

Liley, R. (1962). Some aspects of reproductive isolation in four sympatric species of Poeciliid fishes. - Anim. Behav. 10, p.387-388.

Littlejohn, M.J. (1959). Call differentiation in a complex of seven species of Crinia (Anura, Leptodactylidae). - Evolution 13, p.452-468.

Long, E. & Godfrey, G.F. (1952). The effect of dubbing, environmental temperature and social dominance on mating activity and fertility in the domestic fowl. - Poult. Sci. 31, p.665-673.

Manning, A. (1959a). The sexual isolation between Drosophila melanogaster and D. simulans. - Anim. Behav. 8, p.60-65.

Mayr, E. (1946a). Experiments on sexual isolation in Drosophila. VII: The nature of the isolating mechanism between D. pseudoobscura and D. persimilis. - Proc. Nat. Acad. Sci. 32, 128-137.

Parker, J.E. (1961). Observations on the low fertility problem in Cornish cockerels. - Poult. Sci. 40, 1214-1219.

Parker, J.E., McKenzie, F.F. & Kempster, H.L. (1940). Observations on the sexual behaviour of New Hampshire males.- Poult. Sci. 19, p.191-197.

Philips, A.G. (1919). Preferential mating in fowls. - J.A.A. of I. and I. in Poult. Husb. 5, p.28-30.

Popham, E.J. (1947). Ecological studies of the mating habits of certain species of Corixidae and their significance. - Proc. Zool. Soc. Lond. 116, p.692-706.

Sibley, C.G. (1959). Hybridisation in birds: Taxonomic and evolutionary implications. - Bull. Brit. Orn. Club. 79, p.154-158.

Silson, R.G. (1963). Assortative mating in producing new species. - Nature 197, p.105.

Skard, A.G. (1937). Studies on the psychology of needs: observations and experiments on the sexual needs of hens. - Acta. Psychol. 2, p.175-232.

Taylor, K.F. & Sluckin, W. (1964). Flocking of Domestic Chicks. - Nature 201, p.108-109.

Upp, C.W. (1928). Preferential mating of fowls. - Poult. Sci. 7, p.225-232.

Wood-Gush, D.G.M. (1954). The courtship of the Brown Leghorn Cock. - Anim. Behav. 2, p.95-102.

Wood-Gush, D.G.M. (1956). The agonistic and courtship behaviour of the Brown Leghorn Cock. - Anim. Behav. 4, p.133-142.

Wright, S. (1938). Size of population and breeding structure in relation to evolution. - Science, 87-p.430-431.

Wright, S. (1940). Breeding structure of populations in relation to speciation. - Amer. Nat. 74, p.232-248.